

OCCUPANCY DYNAMICS, PERSONALITY, & BEHAVIOR OF FRANKLIN'S GROUND
SQUIRREL IN AGRICULTURAL LANDSCAPES

BY

JENNIFER M. DUGGAN

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Biology
with a concentration in Ecology, Ethology, and Evolution
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2011

Urbana, Illinois

Doctoral Committee:

Associate Professor Carla E. Cáceres, Chair
Research Professor Edward J. Heske, Director of Research
Assistant Professor Robert L. Schooley, Director of Research
Professor Ken N. Paige

ABSTRACT

Habitat loss and fragmentation are the leading threats to biodiversity worldwide. In fragmented landscapes, movement of organisms among patches of suitable habitat is critical to ecological and evolutionary processes. Movement of organisms allows maintenance of genetic diversity, rescue of declining populations, and recolonization following local extinctions. Connectivity, the degree of movement among patches, is dependent on both the spatial arrangement of habitats, or other landscape elements, and behavioral responses of individuals to physical structure of a landscape. Hence, connectivity for a species is best understood by examining movement at multiple scales. Here, I examine movement of *Poliocitellus franklinii* (Franklin's ground squirrels), a grassland species of conservation concern, at multiple scales in agricultural landscapes in the Midwestern United States.

First, I investigated the relative influence of habitat quality, area, and connectivity on patterns of site occupancy and extinction for *P. franklinii* at the landscape scale. While many methods are used to measure connectivity, debate about which metrics are preferred for applied conservation issues is ongoing. Thus, while investigating occupancy dynamics for *P. franklinii* using 3 years of presence-absence data collected at 55 sites, I also compared predictive performance of Nearest neighbor (NN) and Incidence Function Model (IFM) metrics based on both Euclidean and cost-distances. I found habitat quality, area, and connectivity were all positive predictors for occupancy by *P. franklinii*. Only isolation was a positive predictor of extinction, suggesting connectivity was especially important in allowing dispersers to rescue populations from local extinction. A simple NN metric measuring Euclidean distance between a target patch and nearest occupied source (NS) outperformed IFM metrics (Euclidean and cost-

distance) in predicting occupancy and extinction for *P. franklinii*, indicating simple NN metrics may be adequate when measuring connectivity for rare species with few occupied habitat patches within dispersal distance.

Low densities, secretive behavior, and a tendency to burrow underground in thick grass make it difficult to survey for *P. franklinii*. Therefore, while conducting occupancy surveys for *P. franklinii*, I collaborated with Working Dogs for Conservation to develop use of detection dogs in occupancy surveys for cryptic small mammals. I livetrapped at 62 sites for *P. franklinii* and surveyed 40 of those sites using detection dogs. Independent surveys of a site by 2 dog-handler teams took <1 hr and resulted in detection rates comparable to 2 daily livetrapping surveys (detection rate = 83-84%). Surveys by 2 dog-handler teams can cover more and larger sites in a shorter time than 2 daily livetrapping surveys, with only a moderate increase in cost. I conclude a two-stage strategy could be used effectively in large-scale surveys for a variety of rare and cryptic species, whereby livetrapping is conducted only at sites where detection dog surveys indicate presence.

Next, I used a field experiment to examine movement decisions of adult *P. franklinii* in agricultural landscapes during mating season in the spring. By translocating radiocollared adult squirrels across fallow crop fields and tracking routes home, I tested if individuals based gap-crossing decisions on lengths of alternate movement routes or on individual energetic constraints. I used giving-up densities to determine that *P. franklinii* perceived a higher risk of predation in crop fields than in grass, but travel speed, calculated using telemetry locations, was not strongly adjusted to counteract risk when traveling through crop fields. Squirrels did not appear to base gap-crossing decisions on lengths of alternate movement routes. Instead, body mass was the only predictor of gap crossing; lighter squirrels were more likely than were heavier

squirrels to cross crop fields. The importance of body mass in gap crossing decisions suggests sciurid movements through heterogeneous landscapes are partly explained by trade-offs between predation risk and energetic constraints. Additionally, all squirrels translocated <400 m homed within 24 hrs of release, but likelihood of homing decreased with increasing crossing distance. High homing success suggests *P. franklinii* can be proficient at moving across an agricultural landscape, but the low frequency of field crossing implies fallow fields may be areas of high predation risk that inhibit adult movements and gene flow during the mating season in the spring.

Finally, I examined how variation in individual personality might influence movement and habitat use for *P. franklinii*. I used hole-board tests to characterize personalities of individuals and then related personality to space use by squirrels. *P. franklinii* individuals demonstrated repeatable personalities characterized by vigilance and activity. For radiocollared, juvenile males, individual home range size and length of movements related negatively to vigilance and positively to activity demonstrated during hole-board testing. Findings suggest variation in individual personalities characterized by vigilance and activity can affect space use, and given a positive relationship between home range size and dispersal distance, may potentially influence connectivity and metapopulation dynamics at a larger scale.

ACKNOWLEDGMENTS

This research would not have been possible without the guidance and support of many people. I thank my advisors, Ed Heske and Bob Schooley for the time and effort they have contributed to my education and development as a researcher. I also thank my committee members Ken Paige and Carla Cáceres for their support throughout my graduate career. I am also grateful to my former M.S. advisor, Jay Diffendorfer, for nurturing my interest in conservation biology and for providing me the initial opportunity to pursue an education in this field. I thank my collaborators from Working Dogs in Conservation, Aimee Hurt and Allison Whitelaw, for their valuable contributions to this research. I am grateful to the many reserve managers and private landowners who allowed access to properties for research, especially the Barnhart, Layden, and Smith families. I am also indebted to the hardworking people who helped collect data in the field: L. Buckingham, S. Fredebaugh-Siller, N. Karniski, A. Keever, J. Nachel, H. Pioch, L. Pritchard, J. Rydzewski, J. Strand, and L. Zicarelli. Finally, I am forever grateful to the many friends and family members who have supported me in this endeavor; their encouragement has been integral to my success.

TABLE OF CONTENTS

CHAPTER 1: MODELING OCCUPANCY DYNAMICS OF A RARE SPECIES, FRANKLIN’S GROUND SQUIRREL, WITH LIMITED DATA: ARE SIMPLE CONNECTIVITY METRICS ADEQUATE?.....	1
CHAPTER 2: COMPARING DETECTION DOG AND LIVETRAPPING SURVEYS FOR A CRYPTIC RODENT.....	35
CHAPTER 3: GAP-CROSSING DECISIONS BY FRANKLIN’S GROUND SQUIRREL IN AGRICULTURAL LANDSCAPES	66
CHAPTER 4: PERSONALITY AND SPACE USE IN FRANKLIN’S GROUND SQUIRREL (<i>POLIOCELLUS FRANKLINII</i>).....	95
APPENDIX A.....	121
APPENDIX B.....	123

CHAPTER 1

MODELING OCCUPANCY DYNAMICS OF A RARE SPECIES, FRANKLIN'S GROUND SQUIRREL, WITH LIMITED DATA: ARE SIMPLE CONNECTIVITY METRICS ADEQUATE?¹

ABSTRACT

Conservation of populations in fragmented habitats is often based on spatially realistic metapopulation theory, which predicts negative relationships between patch extinction and area and patch colonization and isolation. Cost-distance metrics have been developed to integrate habitat quality into measures of connectivity, and thus may improve predictive power of the area-isolation paradigm. Few studies use empirical data to compare predictive performance of complex cost-distance metrics to simple metrics relying on Euclidean distances. I used 3 years of presence-absence data to examine relative influence of habitat quality, habitat area, and connectivity on occupancy and extinction rates for *Poliocitellus franklinii* (Franklin's ground squirrel), a rare grassland species of conservation concern. I calculated connectivity using nearest-neighbor (NN) and incidence function model (IFM) metrics based on Euclidean and cost-distances. Habitat quality, area, and connectivity were all positive predictors for occupancy, but only isolation was a positive predictor of extinction. *Poliocitellus franklinii* does not appear to be a tallgrass prairie obligate, but the species distribution is limited by isolation of suitable grassland habitat. A simple NN metric measuring Euclidean distance between a target area and nearest occupied source (NS) outperformed IFM (Euclidean and cost-distance) in predicting

¹This chapter appeared in its entirety in Landscape Ecology as Duggan, J. M., R. L. Schooley, and E. J. Heske. 2011. Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? 26:1477-1490. This article is reprinted with the permission of the publisher (Springer Science + Business Media B. V) and is available from <http://www.springerlink.com> using DOI: 10.1007/s10980-011-9652-9

occupancy and extinction for *P. franklinii*. Although NN metrics are criticized for considering only the contribution of the source nearest to a target, this simplicity may be acceptable when measuring connectivity for rare species with few occupied habitat patches within dispersal distance.

Key words: Incidence function model, cost-distance modeling, metapopulation, Midwestern USA, nearest neighbor, *Poliocitellus franklinii*, *Spermophilus franklinii*, prairie

INTRODUCTION

Habitat loss and fragmentation are the most prevalent threats to biodiversity worldwide (Wilcove et al. 1998). In fragmented landscapes, movement of organisms among remaining patches of suitable habitat is essential for maintaining demographic and genetic connectivity (Hanski and Gaggiotti 2004), and species are often studied using a patch-matrix representation in which an inhospitable matrix restricts such movement (Frank and Wissel 1998; Ovaskainen and Hanski 2004). Where habitat is depicted as either patch or matrix, spatially realistic metapopulation theory predicts probability of patch extinction is related negatively to patch area and probability of patch colonization is related negatively to isolation (Hanski 1994; Hanski and Gaggiotti 2004). However, weak empirical support for the area-isolation paradigm calls into question its utility for biodiversity conservation (Pellet et al. 2007; Prugh et al. 2008).

Poor predictive power of the area-isolation paradigm may be due, in part, to lack of integration of habitat quality into measures of patch area and connectivity (Pellet et al. 2007; Prugh et al. 2008; Schooley and Branch 2009). Quality of habitat patches can influence survival and fecundity, and thus population size. As population size decreases, probability of extinction

increases and availability of dispersers for other patches decreases (Jaquiéry et al. 2008). Habitat quality of patches can influence probability of colonization by attracting or repelling dispersers (Fleishman et al. 2002; Franken and Hik 2004). Further, matrix heterogeneity may affect movements and survival of dispersers (Ricketts 2001) and thus influence probability of colonization and demographic rescue (Brown and Kodric-Brown 1977).

Nearest-neighbor (NN) metrics that use Euclidean distance between a source and target patch are easy to calculate and are widely used to measure connectivity (Prugh et al. 2009). However, NN metrics do not account for source patches beyond the nearest neighbor, or heterogeneity of matrix habitat, and researchers have criticized them as overly simplistic (Moilanen and Nieminen 2002; Bender et al. 2003; Fagan and Calabrese 2006). Nevertheless, Prugh et al. (2009) found one NN metric, Euclidean distance to nearest known occupied source (NS), predicted patch occupancy and colonization as well as a more complex incidence function model (IFM; Hanski 1994) metric. The IFM metric includes distances to, and areas of, all potential source sites, and a parameter scaling the effect of distance on dispersal. Whereas IFM metrics are useful for examining the contribution of specific patches to metapopulation viability (Ovaskainen and Hanski 2001), many applied conservation studies lack the species-specific dispersal data needed to parameterize IFM metrics (Calabrese and Fagan 2004; Prugh 2009). For studies that require only a connectivity metric able to predict occupancy and turnover rates, the NS metric might suffice (Prugh 2009).

Recently, ecologists have applied cost-distance measures of connectivity by assigning movement costs to each type of matrix habitat (i.e., resistance sets) and then calculating least-cost paths between patches (Ferrerias 2001; Magle et al. 2009). When habitat-specific movement rates or preferences are unknown, multiple resistance sets can represent alternative hypotheses

for how a species moves through a heterogeneous matrix that are tested using empirical data on occupancy or turnover (Chardon et al. 2003; Verbeylen et al. 2003; Schooley and Branch 2009). Few studies use empirical data on wildlife distributions to compare performance of NN metrics to cost-distance metrics (but see Magle et al. 2009). Debate about which connectivity metrics are preferred for applied conservation problems (Tischendorf and Fahrig 2000; Fagan and Calabrese 2006) will only be resolved by additional comparisons of metric performance based on empirical data.

I examined the influence of habitat quality, patch area, and connectivity calculated using NN and IFM (Euclidean and cost-distance) metrics on occupancy and turnover for *Poliocitellus franklinii* (Franklin's ground squirrel, formerly *Spermophilus franklinii*; Helgen et al. 2009) in the Midwestern U.S. *Poliocitellus franklinii* occurs at low densities in the Midwest and is state-listed as threatened in Illinois, endangered in Indiana, and a species of special concern in Iowa, Missouri, and Wisconsin. Decline of *P. franklinii* in the Midwest is widely attributed to loss and fragmentation of tallgrass prairie habitat (Benedict et al. 1996; Pergams and Nyberg 2001). Since European settlement, 82-99% of tallgrass prairie has been lost, exceeding loss of any other major ecosystem in North America (Samson and Knopf 1994). However, Huebschman (2007) speculated *P. franklinii* is not a prairie-obligate species despite its association with tall, dense grasses. Prairie grasses in the Midwest are primarily warm-season grasses that grow and reproduce in late summer (Kirt 1998). In contrast, cool-season grasses mature in spring and early summer (Kaufman and Kaufman 2007), are often planted as forage in pastures and cover in roadsides and drainages, and are dominant species in most non-prairie grasslands (USSCS 1975). Because *P. franklinii* requires ample food resources and structural cover during its reproductive season in early summer (Haberman and Fleharty 1972; Huebschman 2007), it seems unlikely the

occurrence of *P. franklinii* is dependent only on cover of warm-season prairie grasses. Grassland habitat in the Midwest occurs in small, isolated patches within an agriculturally dominated matrix (e.g., Johnson and Choromanski-Norris 1992). Occupied patches typically harbor ≤ 20 adult squirrels (Martin et al. 2003; Martin and Heske 2004) and are presumed subpopulations connected via dispersal. I predict connectivity between areas of suitable habitat is at least as influential as patch quality and area on occupancy dynamics of *P. franklinii*. However, information on dispersal of *P. franklinii* through an agricultural matrix is limited. Radiotelemetry data for seven juveniles suggested *P. franklinii* readily move through crop fields, but roads might act as barriers to dispersal (Martin and Heske 2005).

Many rare species present the same conundrum as *P. franklinii*. Data on dispersal distances and movements through matrix habitats are scarce. Yet, the ability to estimate connectivity is needed to predict species distributions and to rank remaining habitat for conservation, restoration, and potential reintroductions. I investigated occupancy dynamics for *P. franklinii* in the Midwestern U.S. for 3 years to help inform management of the species, and also compared performance of simple and complex connectivity metrics. I consider my empirical data representative of data available for many species of conservation concern and my comparison of connectivity metrics applicable to such scenarios. My study had four related objectives. First, I examined effects of landscape features—habitat quality, area, and connectivity—on site occupancy and turnover for *P. franklinii*. Second, I compared predictive performance of NN and IFM metrics. Third, I used cost-distance metrics to evaluate support for alternative hypotheses for movement of *P. franklinii* through an agricultural matrix. Fourth, I clarified habitat associations for *P. franklinii* and determined if site occupancy depended mainly on cover of warm-season prairie grasses.

MATERIALS AND METHODS

STUDY AREA

I conducted research at eight locations in Illinois, Indiana, Iowa, and Missouri where presence of *P. franklinii* was confirmed ≤ 20 years prior to sampling using National Heritage Program databases (Figure 1.1; Appendix A). All locations were in landscapes dominated by corn and soybean fields. After exhaustive on-the-ground reconnaissance, I established 5-8 survey sites with potentially suitable habitat for *P. franklinii* within a 5-km radius (assumed maximum dispersal distance; Martin and Heske 2005) of seven of the locations. At the eighth location in Indiana, the Indiana Department of Natural Resources (DNR) established sites and shared trapping data collected in May 2007 using methods similar to my own (described below). I resurveyed the Indiana sites in 2008 and 2009. I grouped sites in Indiana with adjacent sites in Illinois (Figure 1.1) due to close proximity (~ 4.7 km). I considered suitable habitat for *P. franklinii* to be unmowed grass or tallgrass prairie (remnant or restored) located in prairie reserves or along railroad or roadside rights-of-way (Huebschman 2007). Each survey site consisted of 2 parallel 90-m transects located ~ 10 m apart. Nearest-neighbor distances between sites averaged 2.0 km (range = 0.3-6.5 km).

OCCUPANCY SURVEYS

Each summer (May-August) from 2007 to 2009, I livetrapped 55 sites for 4 consecutive days to document occupancy status for *P. franklinii*. However, Indiana DNR livetrapped sites in Indiana for only 2 days in 2007. I randomized the sequence in which we surveyed the eight locations each year, but surveyed all sites within each location simultaneously. I set 10

Tomahawk live traps (model 202, Tomahawk Live Trap, Tomahawk, Wisconsin) at 10-m intervals on each transect (20 traps per site). I covered traps with vegetation to protect captured squirrels from sun and light rain (traps were not opened during heavy rain). I opened traps baited with peanut butter and sunflower seeds each morning from 0700-0900 hr, checked traps at 3-hr intervals until 1500-1700 hr, and then closed traps for the night. I recorded age (juvenile or adult), sex, reproductive condition, and mass of each captured individual. I uniquely marked individuals within a site by clipping small patches of fur, allowing me to count individuals captured at each site. I handled each squirrel <5 min and released it at the capture site. Procedures followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the University of Illinois Institutional Animal Care and Use Committee.

HABITAT QUALITY AND AREA

During summer 2007, I measured habitat characteristics thought to influence site occupancy by *P. franklinii* (Haberman and Fleharty 1972; Huebschman 2007). Soil texture affects burrow structure and drainage and likely correlates with vegetation cover (Haberman and Fleharty 1972; Martin and Heske 2004; Huebschman 2007). I collected soil samples at points located 30 m and 60 m along each 90-m trapping transect by pounding polyvinyl chloride (PVC) tubes (diameter = 5.1 cm, length = 20 cm) into the ground until flush with the surface, reaching nearly half the maximum depth of *P. franklinii* burrows (average maximum depth = 43 cm; Haberman and Fleharty 1972). After pooling the four samples from each site, I used soil particle analysis to determine the percent clay, silt, and sand of the composite sample (Gee and Bauder 1979).

Vegetation influences food resources and concealment cover available to *P. franklinii* (Haberman and Fleharty 1972; Huebschman 2007). Thus, I recorded plant species cover and structure (vertical = height, horizontal = percent cover of bare ground) at 10 1-m² quadrats placed at 10-m intervals along each transect and averaged estimates for the 20 quadrats sampled at each site. I observed minimal variation in vegetation among years and thus did not resurvey vegetation or soil in 2008 and 2009. I grouped ≥ 100 plant species identified across all sites into four functional groups: woody vegetation (trees and shrubs), forbs, warm-season grasses, and cool-season grasses. Sites were commonly dominated by a single cool-season grass such as smooth brome (*Bromus inermis*) or meadow fescue (*Festuca pratensis*), or a combination of warm-season grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*) and giant fox tail (*Setaria faberi*).

Because habitat quality variables exhibited multicollinearity, I used Principal Components Analysis (PCA) to ordinate soil texture and vegetation cover and structure data (SYSTAT[®] 12, Chicago, Illinois, USA). Percent sand in composite samples varied more among sites ($SD = 21.8$) than did percent silt ($SD = 15.2$) or clay ($SD = 9.1$), so I included percent sand to represent soil texture in the PCA. I included average vegetation height and percent cover of bare ground to represent vegetation structure. Vegetation cover included percent cover by woody vegetation, forbs, smooth brome, meadow fescue, and warm-season grasses. I kept smooth brome and meadow fescue separate because I expected different responses by *P. franklinii* to these two species. Smooth brome is a highly palatable grass (Ogle et al. 2010) used by *P. franklinii* as forage, concealment, and nest material (Haberman and Fleharty 1972), so I expected a positive relationship between occupancy by *P. franklinii* and smooth brome cover. Meadow fescue is less palatable than smooth brome (Ogle et al. 2010) and when infected with

endophytes can produce alkaloids that inhibit feeding by herbivores (Justus et al. 1997).

Therefore, I did not expect a positive relationship between occupancy by *P. franklinii* and meadow fescue cover. Smooth brome and meadow fescue together made up 78% of cool-season grass cover and occurred at 91% (brome) and 52% (fescue) of sites. In contrast, other functional groups were dominated by ≥ 3 species. PCA resulted in three axes that explained 65% of variation, and I used PCA scores from these axes in subsequent analyses. The first axis (H1) was correlated positively with vegetation height, cover by warm-season grasses, and cover of bare ground and correlated negatively with brome cover. The second axis (H2) was correlated positively with sandy soil and negatively with cover by woody vegetation and forbs. The third axis (H3) was correlated positively with brome cover and negatively with fescue cover.

Defining a patch of habitat along a linear railroad or roadside right-of-way was problematic, so I measured habitat area as total area covered by unmowed grass, pasture, alfalfa, or prairie within a 500-m radius circle centered on sampling transects at each site. I considered 500 m an estimate of the maximum distance from which a ground squirrel might encounter my traps (Choromanski-Norris et al. 1989; J.M. Duggan, unpublished data). Although linear habitats sometimes extended beyond the 500-m radius, I considered this limit a better operational definition of habitat area than extending a narrow strip indefinitely. Linear habitats also could be corridors for movement, but such an effect was assessed by my cost-distance metrics of connectivity (see below). I measured habitat area using 2007 Cropland Data Layers (U.S. Department of Agriculture-National Agricultural Statistics Service) in ArcGIS 9.3 (ESRI, Redlands, California, USA). Habitat area ranged from 0.04 to 63.65 ha (median = 7.89 ha).

SPATIAL CONNECTIVITY: NEAREST-NEIGHBOR MEASURES

I measured spatial connectivity of each site using two NN metrics with the Distance Matrix tool (Etherington 2011) in ArcGIS 9.3. The NN metrics were distance to nearest known habitat (i.e., study site) whether or not occupied by *P. franklinii* (NH_i), and distance to nearest known source of *P. franklinii* (NS_i). I defined the nearest known source as the nearest study site at which I detected *P. franklinii* during a given year. Cumulative detection probability after 4 days of trapping was 0.96, so sites without detections were unlikely to be sources. I averaged NS_i from 2007-2009 to obtain an overall NS_i value for each site. For both metrics, I considered only study sites as habitat, although unmowed roadsides were occasionally present and habitat extended beyond trapping transects within a few reserves. However, unmowed grassland other than my trapping sites was uncommon within my 5-km radius sampling areas. Indeed, in some locations I had difficulty locating enough habitat to establish 7 trapping sites; in one location I could establish only 5 sites. Thus, unsampled habitat within my study locations was unlikely to influence my modeling results.

SPATIAL CONNECTIVITY: INCIDENCE FUNCTION AND LEAST-COST MODELS

I measured connectivity of each site using a general IFM that includes a negative exponential dispersal kernel and accounts for distances to and area of potential source sites (Hanski 1994; Moilanen and Nieminen 2002; Prugh 2009). Connectivity (S_i) of site i was defined as

$$S_i = \sum_{j \neq i} \psi_j \exp(-\alpha d_{ij}) A_j^b$$

where ψ_j is the probability site j was occupied during the previous year and could act as a source, α is a parameter scaling the effect of distance on dispersal ($1/\alpha$ is average dispersal distance), d_{ij}

is Euclidean distance between target site i and source site j , A is the area of source site j , and b is a parameter scaling the relationship between abundance and source area.

I calculated S_i separately for each transition period (2007-2008, 2008-2009) and included both measures and their average as covariates in analyses. I calculated S_i by setting ψ_j equal to 0 for source sites in which *P. franklinii* was undetected in both years of a transition period, 0.5 for source sites with detections in one year of a transition period, and 1.0 for source sites with detections in both years of a transition period (Schooley and Branch 2009). I considered *P. franklinii* most likely to move between sites following emergence in early spring when adult males seek prospective mates, and in late summer when juveniles disperse. A site unoccupied during the first year of a transition period but occupied during the second year was colonized between surveys, but exact timing is unknown. The same logic applies to sites in which extinctions occurred during a transition period. To estimate α , I first used cross-species regressions and limited empirical data to develop a plausible range for the parameter. A regression between mean dispersal distance and body mass for 14 ground-dwelling sciurids predicted a dispersal distance of ~500 m for *P. franklinii* (J.M. Duggan, unpublished data), whereas a regression between median dispersal distance and body mass for a broader sample of herbivorous and omnivorous mammals (Sutherland et al. 2000) predicted a dispersal distance of ~1,000 m for *P. franklinii*. Dispersal distances for a small sample of *P. franklinii* in a fragmented agricultural landscape averaged ~2,000 m (Martin and Heske 2004; J. M. Duggan, unpublished data). To test which value of α between 0.002 and 0.0005 (representing average dispersal distances between 500 and 2,000 m) best explained observed occupancy, I modeled occupancy of sites from 2007-2009 as a function of $\exp(-\alpha d)$, where d was the distance to nearest potential source site (Schooley and Branch 2009; Cosentino et al. 2010). I ranked models using

Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). The top-ranked model included α set as 0.0005, so I used this value in subsequent analyses. I set b as 0.5 because emigration is unlikely to scale linearly with habitat area (Moilanen and Nieminen 2002). The effectiveness of S_i as a predictor of patch occupancy and colonization is relatively insensitive to estimates for b (Prugh 2009).

I modified IFM metrics by replacing Euclidean distances (d_{ij}) with effective distances calculated using a Least-cost Paths tool (Etherington 2011) in ArcGIS 9.3. I assigned a movement cost to each matrix habitat to create cost grids, and then calculated least-cost paths among sites. The cumulative cost along each least-cost path represents an effective distance integrating Euclidean distance with movement costs of matrix habitats. I based my cost grids on 2007 Cropland Data Layers with 56 x 56 m cells and used nine land-cover classes (Table 1.1).

My four resistance sets represented alternate hypotheses for movement of *P. franklinii* through a heterogeneous matrix (Table 1.1) that I evaluated with my distribution data. For set R1, resistance was 1 for all habitats to represent a homogeneous matrix and Euclidean distances between sites. For sets R2, R3, and R4, I assigned a value of 1 for grass-pasture habitat, representing easy movement through potentially suitable habitat; an intermediate value of 30 for woodland-shrubland habitat; and a value of 100 for wetlands, open water, and high-intensity development. For set R2 (open connectance), I assigned a value of 10 to agricultural crops, developed open space, and low- and medium-intensity development. Because study locations were in rural areas dominated by row crops, most development was low intensity. Thus, set R2 emphasized low resistance for crop fields and secondary roads. For set R3 (roads as barriers), I retained a value of 10 for agriculture, but assigned a value of 90 to developed open space and low- and medium-intensity development to represent secondary roads as potential barriers to

dispersal. For set R4 (crops as barriers), I retained a value of 10 for developed open space and low- and medium-intensity development, but assigned a value of 90 to agriculture to represent crop fields as potential barriers to movement.

MULTI-SEASON OCCUPANCY MODELS

I used a multi-season occupancy modeling framework that relies on presence-absence data to account for imperfect detection probability (p) and examine how habitat quality, habitat area, and spatial connectivity influenced initial occupancy probability (ψ_{2007}), colonization probability (γ), and extinction probability (ϵ) for *P. franklinii* (MacKenzie et al. 2006). Each day of trapping represented an independent survey, and each 4-day trap session represented a season (i.e., year). I conducted all analyses in Program PRESENCE (3.1) using a logit link function to model effects of covariates on variation among sites for each rate parameter. I normalized all detection, area, and connectivity covariates (mean = 0 and $SD = 1$) prior to analysis.

I conducted initial analyses to select a model accounting for variation in p , while holding ψ_{2007} , γ , and ϵ constant, and included this model in subsequent model sets for ψ_{2007} , γ , and ϵ . Time covariates with potential to influence p included year, Julian date, and day 1-4 of trap session. I also included maximum and minimum daily temperature and daily precipitation (NOAA 2010) as survey-specific covariates and habitat area as a site-specific covariate for detection. Next, I modeled ψ_{2007} , γ , and ϵ sequentially, ranking support for candidate models using AICc (Burnham and Anderson 2002), and including the most supported model for each parameter in subsequent model sets for remaining parameters. For each rate, I first examined support for models including local habitat quality only (H1, H2, H3, H1+H2, H2+H3, H1+H3,

H1+H2+H3). Ranking support for PCA habitat quality axes allowed me to test if *P. franklinii* is a prairie-obligate species requiring high cover of warm-season grasses.

I combined habitat quality covariates from the top-ranked model for each rate with habitat area and connectivity covariates (NH_i , NS_i , R1, R2, R3, R4) to create a set of 28 candidate models, including an intercept-only model. Candidate models included the following covariates: habitat quality, area, connectivity, habitat quality+area, connectivity+area, habitat quality+connectivity, habitat quality+connectivity+area. Due to my moderate sample size, I did not include models with interaction terms in my candidate model set to avoid overparameterization. For each parameter rate, I ran models with IFM and cost-distance covariates calculated for 2007-2008 and 2008-2009 transition periods, and an average of both, and then kept connectivity covariates from top-ranked models to use in my candidate model set.

PERFORMANCE OF CONNECTIVITY METRICS

I compared support for my six connectivity metrics (NH_i , NS_i , R1, R2, R3, R4) by summing Akaike weights across all models within each candidate model set (Burnham and Anderson 2002). Each connectivity metric was in four models for each candidate model set. Comparing summed Akaike weights allowed me to evaluate overall performance of simple and complex metrics in predicting occupancy dynamics of *P. franklinii*, and to test which hypothetical cost surface best explained movement of *P. franklinii*.

RESULTS

I detected *P. franklinii* at 21 sites (naïve occupancy = 38%) in 2007, 17 sites (31%) in 2008, and 15 sites (27%) in 2009. Using single-season occupancy models in which ψ was held

constant, annual probability of occupancy after accounting for imperfect detection was 0.41 ($SE = 0.07$) in 2007, 0.32 ($SE = 0.07$) in 2008, and 0.28 ($SE = 0.06$) in 2009. Of 55 sites, 26 (47%) were never occupied, 13 sites (24%) were occupied during 1 year, 8 sites (15%) were occupied during 2 years, and 8 sites (15%) were occupied during all 3 years. Local colonizations ($n_{2008} = 5$, $n_{2009} = 5$) were outnumbered by local extinctions ($n_{2008} = 9$, $n_{2009} = 7$). Five sites experienced both a colonization and extinction. Using a multi-season occupancy model in which ψ , γ , and ϵ were held constant, colonization probability was 0.14 ($SE = 0.04$) and extinction probability was 0.40 ($SE = 0.08$) after accounting for imperfect detection.

MULTI-SEASON OCCUPANCY MODELS

Competitive models ($\Delta AIC_c \leq 2$) for detection probability included habitat area, daily precipitation, and daily minimum temperature as covariates (Table 1.2). Because a model with negative effects of habitat area (top model: $\beta = -0.42$, $SE = 0.16$) and daily precipitation (top model: $\beta = -0.22$, $SE = 0.15$) on detection rate increased model fit substantially, I included both as covariates for detection in all subsequent models. Estimates of per-survey (i.e., daily) detection rate (p) for each site ranged from 0.23 ($SE = 0.10$) to 0.66 ($SE = 0.05$) with an average value of 0.55 ($SE = 0.06$), indicating I had a 55% chance of capturing *P. franklinii* with one day of livetrapping if the species was present. A competing model for detection included negative effects of habitat area and daily minimum temperature (Table 1.2), but log-likelihood values indicated addition of daily minimum temperature did not substantially improve model fit relative to a model with only habitat area (Burnham and Anderson 2002).

The most supported habitat quality model for initial occupancy included positive effects of PCA axes H1 (warm-season grasses, taller vegetation) and H3 (smooth brome) on occupancy,

indicating site occupancy by *P. franklinii* was not dependent only on high cover of warm-season prairie grasses. A competitive model included H1, H2, and H3, but the addition of H2 did not substantially improve model fit relative to the H1+H3 model. Because I observed only ten colonizations between 2007 and 2009, I did not model effects of habitat quality covariates on colonization rate. The most supported habitat quality model for extinction rate included a positive relationship between extinction and H3. A competitive model for probability of extinction, including H3 plus a negative relationship with H1, did not substantially improve model fit relative to the model including only H3.

The most supported model for initial occupancy included habitat quality (H1+H3), habitat area, and connectivity metric NS_i (Table 1.2). Probability of occupancy related positively to both cover of tall, low-density, warm-season grasses (top model: $\beta = 3.21$, $SE = 1.49$) and cover of the cool-season grass smooth brome (top model: $\beta = 2.65$, $SE = 1.12$; Figure 1.2). Probability of occupancy averaged 0.93 (average $SE = 0.05$, $n = 6$) for sites with $\geq 20\%$ cover by warm-season grasses and 0.56 (average $SE = 0.14$, $n = 35$) for sites with $\geq 20\%$ cover by smooth brome. Probability of occupancy only averaged 0.03 (average $SE = 0.04$, $n = 12$) for sites with $\geq 20\%$ cover by meadow fescue. Site occupancy was related negatively to distance to the nearest known source of *P. franklinii* (top model: $\beta = -0.93$, $SE = 0.58$; Figure 1.2). No sites > 8 km from a known source were occupied, suggesting a possible threshold distance for dispersal. Additionally, the number of individuals trapped on a site related negatively to isolation (NS_i). For sites occupied in 2007, the average distance between a site and the nearest known source of *P. franklinii* was twice as far for sites at which I trapped ≤ 2 individuals (3 km, range = 0.03-6.9 km, $n = 13$) than for sites at which I trapped ≥ 3 individuals (1.5 km, range = 0.03-3.4 km, $n = 8$). Site occupancy demonstrated a positive, albeit weak, relationship with habitat area (top model: β

= 1.04, $SE = 0.62$; Figure 1.2). Competing models for occupancy included a positive relationship between occupancy and the R2 (open connectance) cost-distance metric, but including R2 did not improve model fit relative to models including NS_i (Table 1.2).

Connectivity, as measured by the NS metric, and the percent cover of brome on a site appeared to be the most important factors determining whether *P. franklinii* occupied a site at least once during the 3-yr study. Sites never occupied had a greater median distance to nearest known source ($NS = 4.1$ km) than did sites occupied at least 1 yr ($NS = 2.2$ km). The median percent cover of brome was lower for sites never occupied (24%) than for sites occupied ≥ 1 yr (39%).

Because I observed only ten colonizations between 2007 and 2009, I did not include covariates in models for colonization rate. I included covariates for extinction, but given the moderate sample size ($n = 16$) and degree of model selection uncertainty, results for extinction models should be considered with caution. The most supported model for extinction included the connectivity metric NS_i . Probability of extinction was related positively to distance between a site and the nearest known source of *P. franklinii* (top model: $\beta = 2.89$, $SE = 1.13$; Figure 1.3). PCA axis H3, habitat area, and connectivity metric NH_i , also had positive relationships with extinction in competing models for extinction probability, but none substantially improved model fit (Table 1.2). Probability of extinction related negatively to the number of *P. franklinii* captured at a site. Of 13 occupied sites in 2007 at which I trapped ≤ 2 individuals, 12 (92%) experienced a local extinction in either 2008 or 2009. Of 8 occupied sites in 2007 at which I trapped ≥ 3 individuals, only 1 (13%) experienced a local extinction.

PERFORMANCE OF CONNECTIVITY METRICS

Models including simple NN connectivity metrics were better predictors of occupancy and extinction probabilities than models including IFM metrics calculated using either Euclidean or least-cost distances. Models including NS_i had the most support for predicting occupancy probability ($w_i = 0.44$), followed by models including the R2 cost-distance metric (open connectance; $w_i = 0.29$; Figure 1.4). Other metrics had little support for predicting occupancy ($w_i < 0.05$ for each). Models including NS_i also had the most support for predicting extinction probability ($w_i = 0.51$), followed by models including NH_i ($w_i = 0.36$; Figure 1.4). Other metrics had little support for predicting extinction ($w_i < 0.03$ for each).

DISCUSSION

Grassland habitat, especially tallgrass prairie, is greatly diminished in the Midwestern U.S. (Samson and Knopf 1994). As grasslands continue to be converted to agricultural uses, particularly biofuel production (Fargione et al. 2009), conservation of grassland-dependent species will rely on how occupancy of remaining grassland patches is affected by connectivity. Habitat quality, habitat area, and connectivity all predicted initial occupancy for *P. franklinii*, but only connectivity was an important predictor of local extinction. Less-connected sites had a greater chance of going extinct. Probability of occupancy, and number of individuals trapped, also related negatively to distance between a site and its nearest known source of *P. franklinii*. No sites >8 km from a known source were occupied, suggesting a threshold distance beyond which dispersal between sites is unlikely. Thus, loss of suitable habitat and connectivity both influenced site occupancy by *P. franklinii*, but connectivity was especially important in allowing dispersers to rescue populations from local extinction (Brown and Kodric-Brown 1977).

I found only weak evidence for a relationship between probability of extinction and habitat area. However, extinction probability was related negatively to number of *P. franklinii* captured on a site. This result was not surprising; larger populations are less susceptible to extinctions caused by random demographic or genetic threats (Mills 2006). Because *P. franklinii* is one of the least social ground squirrels and is distributed sporadically in small colonies (Murie 1999), the expected relationship between area and population size (underlying area-extinction predictions) may not be strong. Furthermore, because my study sites were similar in size or smaller than home ranges, local colonizations and extinctions do not necessarily indicate turnover of entire colonies of individuals, but rather changes in resource use at a patch scale (MacKenzie et al. 2006).

My NN connectivity metrics outperformed more complex IFM metrics in predicting occupancy and extinction probabilities for *P. franklinii*. A meta-analysis by Prugh (2009) also found NS could outperform IFM metrics in predicting occupancy and colonization rates. In contrast, Magle et al. (2009) reported that IFM metrics modified to include costs of movement through a heterogeneous matrix outperformed a nearest-habitat (my NH) metric, but did not consider NS. Unlike the prairie dogs (*Cynomys ludovicianus*) studied by Magle et al. (2009), *P. franklinii* was rare within my study area, with little suitable habitat available for occupancy.

I suggest NN metrics (particularly NS) might outperform IFM metrics in studies of rare species for two main reasons. First, performance of IFM metrics is sensitive to estimates of the α parameter (Moilanen and Nieminen 2002; Prugh 2009). Estimation of α is likely to be associated with considerable uncertainty when dispersal data are limited for a species. Pellet et al. (2007) and Prugh (2009) suggested using model fitting to estimate α from occupancy data, and this approach has been successfully applied to rare species (e.g., Schooley and Branch 2009).

Nevertheless, a model-fitting approach does not guarantee a biologically meaningful measure of α . I considered running sensitivity analyses based on α -values estimated from cross-species regressions, and the limited dispersal data available for *P. franklinii*, to be a reasonable approach. I expect many researchers will have to work with similarly limited data. A model is only as good as the data used to construct it; my results emphasize this point. Second, NN metrics are criticized for considering only the contribution of the patch nearest to a target patch (Bender et al. 2003; Calabrese and Fagan 2004), but this simplicity may not be detrimental when suitable habitat patches, particularly occupied patches, are seldom within dispersal distance. In extremely fragmented landscapes such as mine with little remaining grassland habitat, the nearest-neighbor patch is likely the main source of colonists.

Although site occupancy by *P. franklinii* was best predicted by models including the NS connectivity metric, the R2 (open connectance) cost-distance metric was in competitive models. The R2 cost-distance metric had low costs of movement through agricultural crops and developed habitats with impervious surfaces covering < 80% land area, but high costs of movement where impervious surfaces covered > 80% land area. Industrial areas and highways likely presented barriers to movements of *P. franklinii* according to these models, but crop fields and secondary roads did not (see also Martin and Heske 2005). Future studies should evaluate how road size and traffic density hinder movements of *P. franklinii*. It is not surprising row crops are not barriers to movement of dispersing juveniles in late summer and autumn when crops are at full height. However, if barren crop fields impede movement, earlier harvests in the Midwest predicted by some scenarios of global climate change (Southworth et al. 2000) could affect dispersal of *P. franklinii*.

Poliocitellus franklinii has been referred to as a prairie-obligate species in the southern portion of its range (Benedict et al. 1996; Pergams and Nyberg 2001), but my analyses indicate other grasslands are also suitable habitats. Probability of occupancy related positively to cover of tall, warm-season prairie grasses and cover of the cool-season grass, smooth brome. Thus, *P. franklinii* occupancy was not solely dependent on the presence of warm-season prairie habitat, and my data support the contention of Huebschman (2007) that categorization of *P. franklinii* in the Midwestern U.S. as a “prairie species” is a misconception. Given the limited availability of prairie habitat in my study area, *P. franklinii* also may resort to using more abundant brome habitat where warm-season prairie no longer exists. Some researchers speculate that unmowed roadside rights-of-way might often represent the only available habitat meeting *P. franklinii*’s needs in the southern portion of its range (Huebschman 2007 and references therein).

However, habitat selection by *P. franklinii* is likely more complicated than a simple choice of warm-season prairie versus cool-season grassland. Habitats dominated by cool-season grasses offer plentiful cover in spring and early summer and high-energy seeds and fruits needed by individuals for reproduction. As the season progresses, however, cool-season grasses become less productive. Ground squirrels preparing for hibernation in areas without food resources providing sufficient nutrition in late summer and fall may either relocate or face local extinction (Sherman and Runge 2002), as suggested by the positive relationship between extinction and cover of cool-season grasses in some of my models. A mix of the two types of grasses, or at least proximity, may be necessary for year-round occupancy. Although other types of vegetation that could provide resources in spring or fall, and soil texture that affects drainage, did not emerge as strong predictors of occupancy in my analyses, these factors along with local topography may mitigate habitat quality for *P. franklinii* (Martin and Heske 2004; Huebschman

2007). Detailed studies of seasonal resource use by *P. franklinii* may further elucidate how local habitat quality interacts with connectivity to influence the spatial distribution of this rare species.

ACKNOWLEDGMENTS

I thank the Indiana DNR for sharing trapping data. I am grateful to D. Bautz, J. Flinn, and S. Ingram for assistance finding historical locations of *Poliocitellus franklinii* and to managers of Barnhart Prairie Nature Preserve, Bilby Ranch Lake Conservation Area, Scuppernong Prairie State Natural Area, and private landowners for allowing access to properties. I am especially grateful to N. Karniski, M. McNicoll, J. Nachel, H. Pioch, J. Strand, and L. Ziccarelli for field assistance and R. Darmody for help with soil particle analyses. This project was funded by the Illinois DNR through the Federal Aid in Wildlife Restoration Program (Project W-152-R), University of Illinois, Illinois State Academy of Sciences, American Society of Mammalogists, and American Museum of Natural History.

REFERENCES

- BENDER, D. J., L. TISCHENDORF, L. FAHRIG. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* 18:17–39.
- BENEDICT, R. A., P. W. FREEMAN, H. H. GENOWAYS. 1996. Prairie legacies- mammals. Pp. 149-166 in *Prairie conservation: preserving North America's most endangered ecosystem* (F. B. Samson and F. L. Knopf, eds.). Island Press, Washington D.C.
- BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CALABRESE, J.M., AND W. F. FAGAN. 2004. A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment* 2:529–536.
- CHARDON, J. P., F. ADRIAENSEN, AND E. MATTHYSEN. 2003. Incorporating landscape elements into a connectivity measure: a case study for the speckled wood butterfly (*Parargeaegeria* L.). *Landscape Ecology* 18:561–573.
- CHOROMANSKI-NORRIS, J., E. K. FRITZELL, AND A. B. SARGEANT. 1989. Movement and habitat use of Franklin's ground squirrels in duck-nesting habitat. *Journal of Wildlife Management* 53:324-331.
- COSENTINO, B. J., R. L. SCHOOLEY, AND C. A. PHILLIPS. 2010. Wetland hydrology, area, and isolation influence spatial turnover of the painted turtle, *Chrysemys picta*. *Landscape Ecology* 25:1589-1600.

- ETHERINGTON, T. R. 2011. Python based GIS tools for landscape genetics: visualizing genetic relatedness and measuring landscape connectivity. *Methods in Ecology and Evolution* 2:52-55.
- FAGAN, W. F., AND J. M. CALABRESE. 2006. Quantifying connectivity: balancing metric performance with data requirements. Pp. 297-317 in *Connectivity conservation* (K. R. Crooks and M. Sanjayan, eds.). Cambridge University Press, Cambridge, United Kingdom.
- FARGIONE, J. E., T. R. COOPER, D. J. FLASPOHLER, J. HILL, C. LEHMAN, T. MCCOY, S. MCLEOD, E. J. NELSON, K. S. OBERHAUSER, AND D. TILMAN. 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. *BioScience* 59:767-777.
- FERRERAS, P. 2001. Landscape structure and asymmetrical interpatch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation* 100:125–136.
- FLEISHMAN, E., C. RAY, P. SJÖGREN-GULVE, C. L. BOGGS, AND D. D. MURPHY DD. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* 16:706–716.
- FRANK, K., AND C. WISSEL. 1998. Spatial aspects of metapopulation survival – from model results to rules of thumb for landscape management. *Landscape Ecology* 13:363-379.
- FRANKEN, R. J., AND D. S. HIK. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *Journal of Animal Ecology* 73:889–896.
- GEE, G. W., AND J. W. BAUDER. 1979. Particle size analysis by hydrometer: a simplified method for routine textural analysis and a sensitivity test of measurement parameters. *Soil Science Society of America Journal* 43:1004-1007.

- HABERMAN, C. G., AND E. D. FLEHARTY. 1972. Natural history notes on Franklin's ground squirrel in Boone County, Nebraska. *Transactions of the Kansas Academy of Science* 74:76-80.
- HANSKI, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63:151-162.
- HANSKI, I., AND O. E. GAGGIOTTI. 2004. *Ecology, evolution, and genetics of metapopulations*. Academic Press, San Diego, California.
- HANSKI, I., J. ALHO, AND A. MOILANEN. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239-251.
- HELGEN, K. M., F. R. COLE, L. E. HELGEN, AND D. E. WILSON. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. *Journal of Mammalogy* 90:270-305.
- HUEBSCHMAN, J. J. 2007. Distribution, abundance, and habitat associations of Franklin's ground squirrel (*Spermophilus franklinii* Sabine 1822). *Illinois Natural History Survey Bulletin* 38:1-57.
- JAQUIÉRY, J., J. GUÉLAT, T. BROQUET, L. BERSSET-BRÄNDLI, E. PELLEGRINI, R. MORESI, A. H. HIRZEL, AND N. PERRIN. 2008. Habitat-quality effects on metapopulation dynamics in greater whitetoothed shrews, *Crocidura russula*. *Ecology* 89: 2777-2785.
- JOHNSON, S. A., AND J. CHOROMANSKI-NORRIS. 1992. Reduction in the eastern limit of the range of the Franklin's ground squirrel (*Spermophilus franklinii*). *American Midland Naturalist* 128:325-331.
- JUSTUS, M., L. WITTE, AND T. HARTMANN. 1997. Levels and tissue distribution of loline alkaloids in endophyte-infected *Festuca pratensis*. *Phytochemistry* 44:51-57.

- KAUFMAN, S. R., AND W. KAUFMAN. 2007. Invasive plants: a guide to identification and the impacts and control of common North American species. Stackpole Books, Mechanicsburg, Pennsylvania.
- KIRT, R. R. 1998. Prairie plants of the Midwest: identification and ecology. 4th ed. Stipes Publishing L.L.C., Champaign, Illinois.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling. Academic Press, San Diego, California.
- MAGLE, S. B., D. M. THEOBALD, AND K. R. CROOKS. 2009. A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landscape Ecology* 24:267-280.
- MARTIN, J. M., AND E. J. HESKE. 2004. Cover and soil drainage influence burrow location of Franklin's ground squirrel (*Spermophilus franklinii*) in Champaign County, Illinois. *Transactions of the Illinois State Academy of Science* 97:227-233.
- MARTIN, J. M., AND E. J. HESKE. 2005. Juvenile dispersal of Franklin's ground squirrel (*Spermophilus franklinii*) from a prairie "island". *American Midland Naturalist* 153:444-449.
- MARTIN, J. M., E. J. HESKE, AND J. E. HOFMANN. 2003. Franklin's ground squirrel in Illinois: a declining prairie mammal? *American Midland Naturalist* 150:130-138.
- MILLS, L. S. 2006. Conservation of wildlife populations: demography, genetics and management. Blackwell Publishing, Oxford, United Kingdom.
- MOILANEN, A., AND M. NIEMINEN. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131-1145.

- MURIE, J. O. 1999. Franklin's ground squirrel, *Spermophilus franklinii*. Pp. 419-420 in The Smithsonian book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution Press, Washington, D.C.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 2010. National Climatic Data Center. Daily temperature and precipitation data. Available from <http://www7.ncdc.noaa.gov/IPS/coop/coop.html> (accessed September 2010).
- OGLE, L., L. ST. JOHN, AND K. JENSEN. 2010. Species selection and grazing management guidelines. Pp. 7-20 in Pasture and grazing management in the Northwest, PNW 614 (G. E. Shewmaker and M. G. Bohle, eds.). University of Idaho Extension, Moscow.
- OVASKAINEN, O., AND I. HANSKI. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theoretical Population Biology* 60:281-302.
- OVASKAINEN, O., AND I. HANSKI. 2004. Metapopulation dynamics in highly fragmented landscapes. Pp. 73-103 in *Ecology, genetics, and evolution of metapopulations* (I. Hanski and O. E. Gaggiotti, eds.). Elsevier Academic Press, Burlington, San Diego, London.
- PELLET, J., E. FLEISHMAN, D. S. DOBKIN, A. GANDER, AND D. D. MURPHY. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation* 136:483-495.
- PERGAMS, O. R. W., AND D. NYBERG. 2001. Museum collections of mammals corroborate the exceptional decline of prairie habitat in the Chicago region. *Journal of Mammal* 82:984-992.
- PRUGH, L. R., K. E. HODGES, A. R. E. SINCLAIR, AND J. S. BRASHARES. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America* 105:20770-20775.

- PRUGH, L. R. 2009. An evaluation of patch connectivity measures. *Ecological Applications* 19:1300–1310.
- RICKETTS, T. H. 2001 The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- SAMSON, F., AND F. KNOPF. 1994. Prairie conservation in North America. *BioScience* 44:418–421.
- SCHOOLEY, R. L., AND L. C. BRANCH. 2009. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecological Applications* 19:1708–1722.
- SHERMAN, P. W., AND M. C. RUNGE. 2002. Demography of a population collapse: the Northern Idaho ground squirrel (*Spermophilus brunneus brunneus*). *Ecology* 83:2816–2831.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SOUTHWORTH, J., J. C. RANDOLPH, M. HABECK, O. C. DOERING, R. A. PFEIFER, D. G. RAO, AND J. J. JOHNSTON. 2000. Consequences of future climate change and changing climate variability on maize yields in the midwestern United States. *Agriculture Ecosystems and Environment* 82:139–158.
- SUTHERLAND, G. D., A. S. HARESTAD, K. PRICE, AND K. P. LERTZMAN. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4:16. Available from <http://www.consecol.org/vol4/iss1/art16> (accessed September 2010).

- TISCHENDORF, L., AND L. FAHRIG. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7–19.
- U.S. SOIL CONSERVATION SERVICE. 1975. Engineering field manual for conservation practices. U.S. Government Printing Office. Washington D.C.
- VERBEYLEN, G., L. DE BRUYN, F. ADRIAENSEN, AND E. MATTHYSEN. 2003. Does matrix resistance influence red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? *Landscape Ecology* 18:791-805.
- WILCOVE, D. S., D. ROTHSTEIN, J. DUBOW, A. PHILLIPS, AND E. LOSOS. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–615.

TABLES AND FIGURES

Table 1.1 Sets of movement costs for land-cover classes used in cost-distance modeling of spatial connectivity for *Poliocitellus franklinii* at 55 sites in the Midwestern U.S. R1 = Euclidean distances, R2 = open connectance, R3 = roads as barriers, and R4 = crops as barriers

Land-cover class	Resistance sets			
	R1	R2	R3	R4
Grass-pasture	1	1	1	1
Agriculture*	1	10	10	90
Woodlands-shrublands**	1	30	30	30
Developed open space [†]	1	10	90	10
Low-intensity development ^{††}	1	10	90	10
Medium-intensity development [‡]	1	10	90	10
High-intensity development ^{‡‡}	1	100	100	100
Wetlands	1	100	100	100
Open water	1	100	100	100

*All row crops

**Forest, woodlands, shrublands, Christmas tree farms, and orchards

[†]Impervious surfaces cover <20% land area (e.g., parks, lawns, golf courses)

^{††}Impervious surfaces cover 20-49% land area (e.g., single family homes, barns, secondary roads with associated trees and grasses)

[‡]Impervious surfaces cover 50-79% land area (e.g., single family homes, barns, secondary roads)

^{‡‡}Impervious surfaces cover ≥80% land area (e.g., apartment buildings, industrial areas, interstate highways)

Table 1.2 Model selection statistics for detection, initial occupancy, and extinction probabilities of *Poliocitellus franklinii* from 55 sites in the Midwest region. I estimated initial occupancy probability for 2007 and other rates for 2007-2009 (see subscripts)

Rate parameter	Model	ΔAIC_c	ω_i	$-2\text{Log}(L)$	k
Detection ₂₀₀₇₋₂₀₀₉	Area+precipitation	0.00	0.18	432.07	6
	Area	0.60	0.14	434.67	5
	Precipitation	1.37	0.09	435.44	5
	Area+minimum temperature	1.66	0.08	433.73	6
	Intercept only	2.02	0.07	438.09	4
Occupancy ₂₀₀₇	H1+H3+area+NS	0.00	0.28	409.82	10
	H1+H3+NS	1.02	0.17	412.84	9
	H1+H3+area+R2	1.20	0.15	411.02	10
	H1+H3+R2	1.43	0.13	413.25	9
	Intercept only	14.25	0.00	432.07	6
Extinction ₂₀₀₇₋₂₀₀₉	NS	0.00	0.21	399.99	11
	NH	0.75	0.15	400.74	11
	NS+H3	1.06	0.12	399.05	12
	NS+area	1.22	0.12	399.21	12
	NH+H3	1.46	0.10	399.45	12
	Intercept only	7.83	0.00	409.82	10

H1, H2, and H3 represent three PCA habitat quality axes. NS = nearest known source of *P. franklinii*, and NH = nearest known habitat whether or not occupied by *P. franklinii*. R2 represents a resistance set used in cost-distance modeling of spatial connectivity (see Table 1.1). Summary statistics include difference between model AIC_c and lowest AIC_c (ΔAIC_c), Akaike weights (ω_i), twice the negative log-likelihood ($-2\text{Log}[L]$), and number of parameters (k). We present models with $\Delta AIC_c \leq 2$, as well as the intercept model, for each parameter

Figure 1.1 Eight locations where I established 55 study sites in the Midwestern U.S. to survey for presence of *Poliocitellus franklinii* (2007-2009). Inset shows 8 study sites in Champaign, IL. Each site is surrounded by a 5-km radius buffer. Circle = squirrels undetected at site in all years, square = detected in 1 year, triangle = detected in 2 years, and cross = detected all 3 years

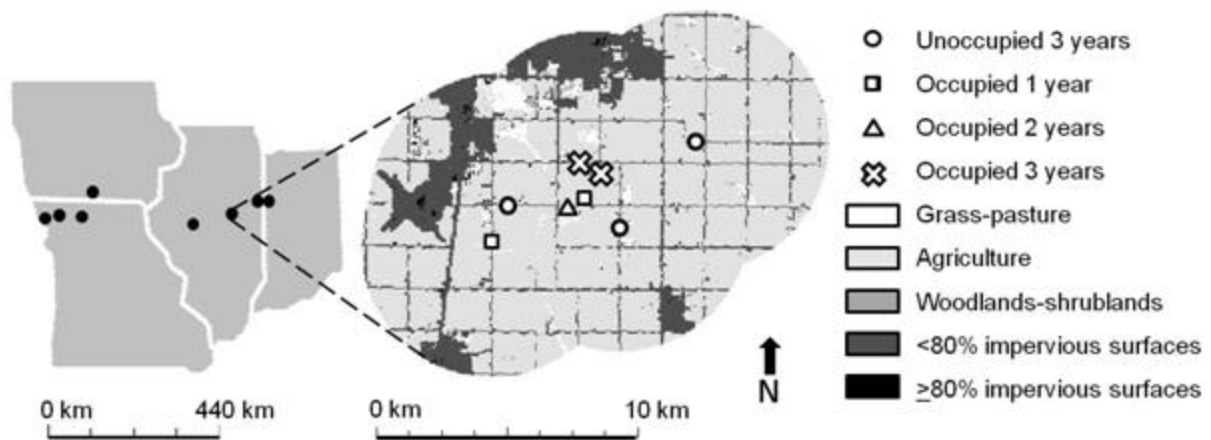


Figure 1.2 Relationship of initial occupancy probabilities of sites by *Poliocitellus franklinii* in 2007 with (a) H1 PCA scores, (b) H3 PCA scores, (c) distance from site to nearest known source of *P. franklinii* (NS), and (d) habitat area. Open circles = initial occupancy probabilities of 55 sites estimated by top-ranked, multiseason occupancy model (see Table 1.2). Closed circles = detection (1) or absence (0) of *P. franklinii* at sites

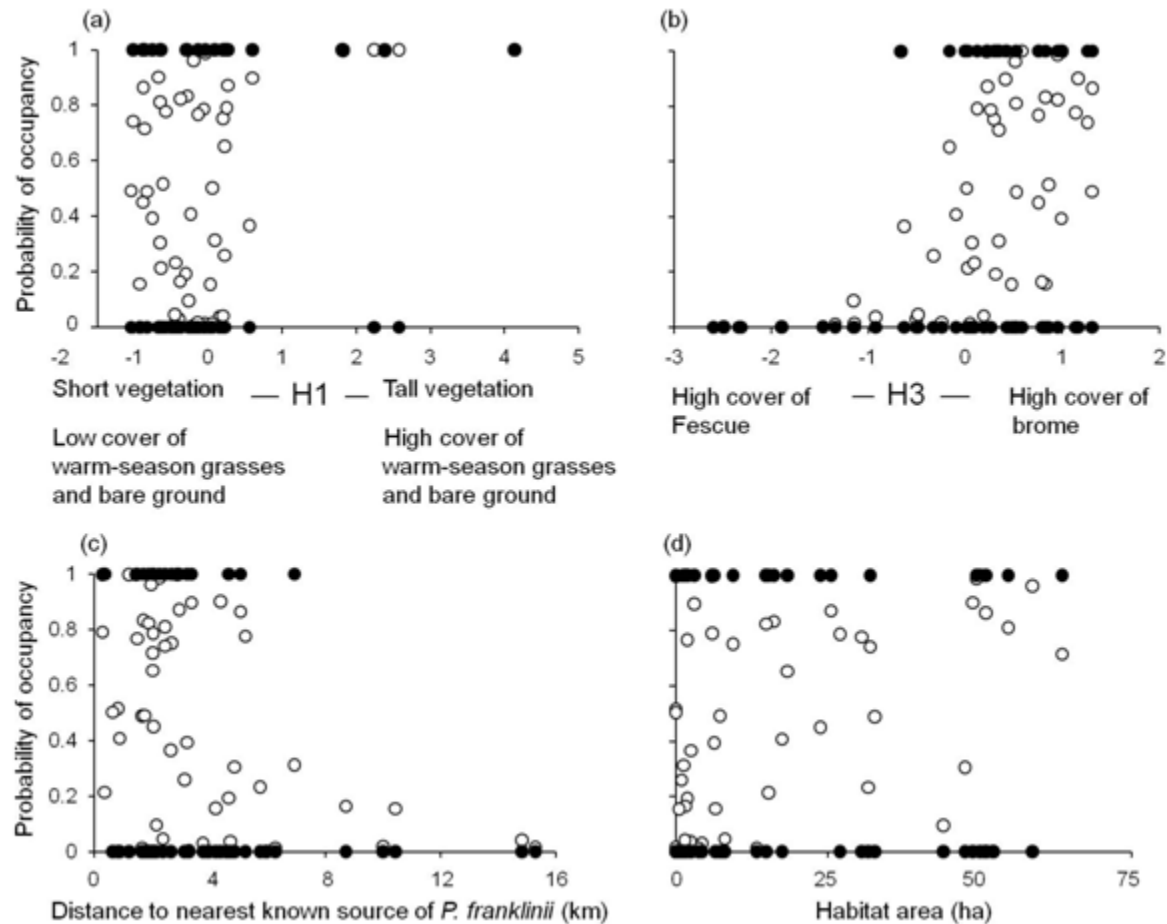


Figure 1.3 Relationship of extinction probabilities of sites by *Poliocitellus franklinii* from 2007-2009 with distance from site to nearest known source of *P. franklinii* (NS). Open circles = extinction probabilities of 55 sites estimated by top-ranked, multiseason occupancy model. Closed circles = observed extinction (1) or no extinction (0) of *P. franklinii* at sites in 2008 and 2009

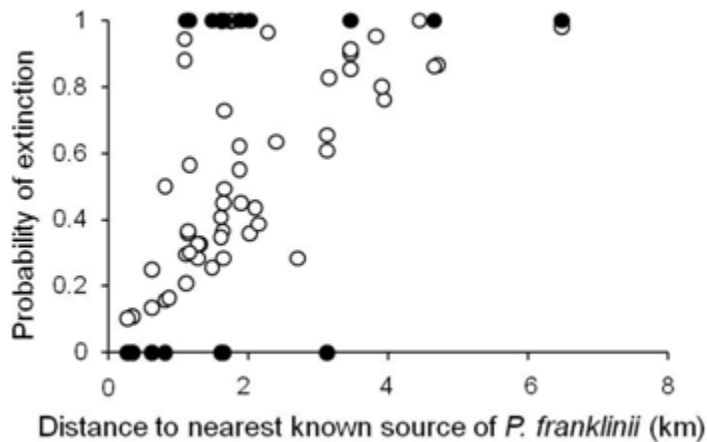
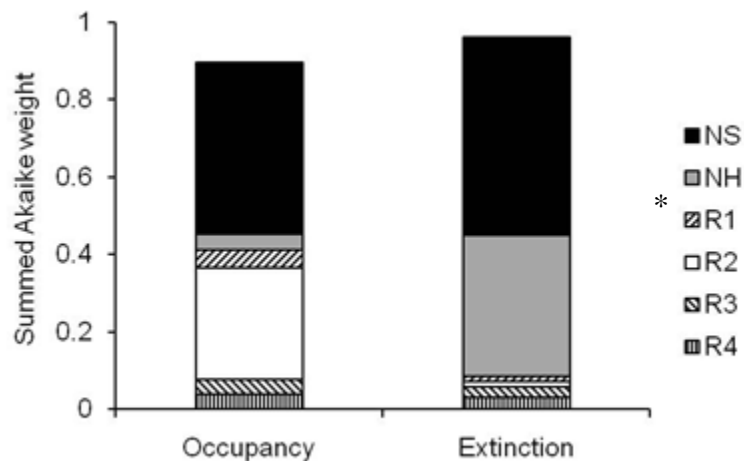


Figure 1.4 Relative support of six connectivity metrics for predicting occupancy and extinction probabilities for *Poliocitellus franklinii* at 55 sites from 2007-2009 based on summed Akaike weights. NS = nearest known source of *P. franklinii*, NH = nearest known habitat, whether or not occupied by *P. franklinii*, R1 = Euclidean resistance set, R2 = open connectance, R3 = roads as barriers, and R4 = crops as barriers (see Table 1.1 for movement costs for resistance sets)



CHAPTER 2

COMPARING DETECTION DOG AND LIVETRAPPING SURVEYS FOR A CRYPTIC RODENT²

ABSTRACT

I compared the effectiveness and cost of distribution surveys using livetrapping to those using detection dog-handler teams for a cryptic rodent (Franklin's ground squirrel, *Poliocitellus franklinii*). I livetrapped at 62 sites in Illinois, Indiana, Iowa, Missouri, and Wisconsin for Franklin's ground squirrels in 2007-2009, and surveyed 40 of those sites using detection dogs in 2009. Independent surveys of a site by 2 dog-handler teams took <1 hr and yielded detection rates comparable to 2 daily livetrapping surveys (detection rate = 83-84%). However, false presences are a potential problem when detection dogs are trained to scent of a species that leaves little visual sign to confirm its presence. Surveys by 2 dog-handler teams cost more than 2 daily livetrapping surveys conducted by 2 technicians, but more and larger sites can be surveyed by dog-handler teams in a shorter time. For surveys covering large spatial scales or when time is a limiting factor, number of false presences and study costs can be reduced by employing a two-stage survey protocol in which livetrapping is conducted only at sites where detection dog surveys indicate presence. I conclude a two-stage strategy could be used effectively in large-scale surveys for a variety of rare and cryptic species.

²This chapter appeared in its entirety in the Journal of Wildlife Management as Duggan, J. M., E. J. Heske, R. L. Schooley, A. Hurt, and A. Whitelaw. 2011. Comparing detection dog and livetrapping surveys for a cryptic rodent. 75:1209-1217. This material is reproduced with permission of John Wiley & Sons, Inc. and is available from <http://www.bioone.org> through The Wildlife Society using DOI: 10.1002/jwmg.150

Key words: cost comparison, detection dog, detection rate, Franklin's ground squirrel, occupancy model, *Poliocitellus franklinii*

INTRODUCTION

Wildlife biologists who monitor and study rare species face difficulties locating study organisms and gathering sample sizes large enough for robust statistical analysis (Gaston 1994). These difficulties can cause biologists to expend considerable effort unproductively, or to abandon studies of uncommon species entirely, leaving rare species vulnerable to inefficient or uninformative research. Yet, it is often rare species that most need scientifically informed conservation. Effective survey methods are needed that can be implemented with minimal labor and cost.

Detection dogs have long been used in police work (Rebmann et al. 2000, Slabbert and Odendaal 1999) and search and rescue missions (Denver et al. 2007), but recently conservation biologists developed methods for surveying species that are cryptic or occur at low densities using trained detection dogs (Hurt and Smith 2009). Detection dogs are used to help biologists locate plants (Goodwin et al. 2010), reptiles (Cablak and Heaton 2006), birds (Robertson and Fraser 2009), and mammals (Reindl-Thompson et al. 2006, Gsell et al. 2010), as well as wildlife carcasses (Homan et al. 2001, Arnett 2006) and scat (Rolland et al. 2006, MacKay et al. 2008, Dematteo et al. 2009). Trained detection dogs potentially can locate species more efficiently than field biologists using traditional survey methods such as livetrapping. For example, dogs trained to detect presence of the endangered black-footed ferret (*Mustela nigripes*) can survey an average of 26 ha/hr (Reindl-Thompson et al. 2006). Besides their ability to cover large areas quickly, detection dogs also can have higher rates of detection than traditional survey methods

(Harrison 2006, MacKay et al. 2008, Nussear et al. 2008, Goodwin et al. 2010). Long et al. (2007a) reported the probability of detecting black bears (*Ursus americanus*) during a single survey of a site was greater using a detection dog-handler team (0.87) than using either remote cameras (0.33) or hair snares (0.08). Per-survey detection rates for dog-handler teams also were higher than remote cameras for fishers (*Martes pennanti*: dogs = 0.84, cameras = 0.28) and bobcats (*Lynx rufus*: dogs = 0.27, cameras = 0.13). Surveys for mammals using detection dogs have been applied primarily to medium- and large-sized carnivores that leave large scat available for detection (MacKay et al. 2008). Effectiveness of detection dogs has rarely been quantified for small mammals that leave less obvious sign above ground (Gsell et al. 2010).

I used trained detection dogs to conduct surveys for Franklin's ground squirrels (*Poliocitellus franklinii*). Although Franklin's ground squirrels occur throughout the central United States and southern Canadian Plains, the species occurs at low densities in the Midwestern United States and is state-listed as threatened in Illinois, endangered in Indiana, and a species of special concern in Iowa, Missouri, and Wisconsin. In the central United States, dense grassland vegetation with which Franklin's ground squirrels is associated occurs in relatively small and isolated patches within an agriculturally-dominated matrix (Johnson and Choromanski-Norris 1992, Martin and Heske 2004). Occupied patches typically harbor ≤ 20 adults (Johnson and Choromanski-Norris 1992, Martin et al. 2003; Martin and Heske 2004) and are presumed subpopulations connected via dispersal with extinction-colonization dynamics described by metapopulation or source-sink models (Hanski and Gaggiotti 2004). Low densities, secretive behavior, and a tendency to burrow underground in thick vegetation make it difficult to survey for Franklin's ground squirrels. Surveys for Franklin's ground squirrels have relied on researchers searching areas of suitable habitat for burrows or other sign, livetrapping for several

days, or both (Johnson and Choromanski-Norris 1992, Martin et al. 2003). These methods are time and labor intensive, and trapping often is limited to a portion of the area potentially suitable for Franklin's ground squirrels. Thus, a survey method that allows rapid assessment of larger areas of habitat would be particularly useful for this cryptic species.

Surveys for Franklin's ground squirrels using detection dogs face unique challenges. First, the small size of Franklin's ground squirrels (adult body mass = 340-800 g; Hofmann 2008), combined with burrowing habits and preference for tall, dense vegetation likely provide detection dogs with weaker or more diffuse scent than that provided by large, terrestrial animals (Gutzwiller 1990, Cablk and Heaton 2006). Second, variation in diet affects the scent of scat. Dogs trained to detect scat samples from an omnivorous species, such as Franklin's ground squirrel, might require exposure to a greater diversity of scat samples than dogs trained to detect scat samples from a species with a specialized carnivorous or herbivorous diet (Smith et al. 2003). Third, Franklin's ground squirrels can be located near populations of thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and therefore detection dogs must distinguish between two similar species. Last, because of the secretive behavior of squirrels and small size of their scats that often are deposited underground in burrows, species' presence cannot usually be confirmed by sighting of an individual or its scat. False positives (i.e., alerting to a squirrel's presence when no squirrels are actually present) are possible for detection dogs, and if a dog is rewarded for a false positive alert, it learns to repeat the error.

I had three main objectives: (1) develop methods for use of detection dogs in occupancy surveys for Franklin's ground squirrels and other cryptic small mammals, (2) compare effectiveness of detection dog and livetrapping surveys, and (3) compare costs of detection dog and livetrapping surveys. I predicted detection rate of Franklin's ground squirrels by detection

dog-handler teams (hereafter referred to as dog teams) would be greater than detection rate by livetrapping, and cost of a detection dog survey would be greater than a livetrapping survey. However, given the greater efficiency of dog teams, I expected more sites could be surveyed per unit time using detection dog surveys than livetrapping.

METHODS

STUDY AREA

The study area consisted of nine locations throughout Illinois, Indiana, Iowa, Missouri, and Wisconsin where presence of Franklin's ground squirrels was confirmed within 10 years prior to sampling. I established 5-8 survey sites with potentially suitable habitat for Franklin's ground squirrels (Huebschman 2003) within a 5-km radius (assumed maximum dispersal distance; Martin and Heske 2004) of each historical location. The 62 total sites were located in prairie reserves, remnant prairie habitat or grasslands along railroad rights-of-way, or in grassy roadside rights-of-way. Sites were set across a range of environmental variables with potential to affect occurrence of Franklin's ground squirrels (i.e., plant species composition, vegetation height, and distance to nearest road).

OCCUPANCY SURVEYS VIA LIVETRAPPING

Each summer (May-August) from 2007-2009, I livetrapped all 62 sites for 4 consecutive days. Surveys for Franklin's ground squirrels are typically conducted in 2 or 3-day trap sessions (Johnson and Choromanski-Norris 1992, Martin et al. 2003). However, I extended sessions to 4 days to increase precision of occupancy estimates for a separate study modeling habitat use of Franklin's ground squirrels. I did not survey sites randomly due to logistical constraints.

Because sites were grouped around nine locations where Franklin's ground squirrels were historically present, instead I randomized the sequence in which I surveyed groups each year. A site consisted of 2 parallel transects set ~10 m apart, each with 10 Tomahawk collapsible live traps (model 202, Tomahawk Live Traps, Inc., Tomahawk, Wisconsin) set at 10-m intervals (total of 20 traps per site). The size of study sites was limited by available potential habitat because stretches of unmowed, roadside rights-of-way rarely surpassed 100 m in length. I covered each trap with vegetation to protect captured squirrels from sun and light rain (traps were not opened during heavy rain). I opened traps baited with peanut butter and sunflower seeds each morning from 0700-0900 h and checked traps at 3-hr intervals until 1500-1700 h. I then closed all traps for the night. Handling of each squirrel lasted <5 min and all animals were released at the site of capture. All procedures followed animal care and use guidelines approved by the American Society of Mammalogists (Sikes et al. 2001) and were approved by the University of Illinois Institutional Animal Care and Use Committee (Protocol #07071).

I used occupancy modeling procedures (MacKenzie et al. 2006) with Program PRESENCE (http://www.mbr-pwrc.usgs.gov/software/bin/setup_presence.zip) to estimate probability of detection (p), given presence, using presence-absence data collected over 3 years of livetrapping. I ran multi-season models with each day of trapping representing an independent survey (i.e., 4 surveys each year per site) and each 4-day trap session representing a "season" (i.e., year). I included survey-specific covariates with potential to influence detection probability, such as year, day 1-4 of trap session, and Julian date. I also included detection covariates derived from information retrieved from the National Oceanic and Atmospheric Administration's National Climatic Data Center including maximum and minimum daily temperature and daily precipitation. I normalized continuous covariates (mean = 0 and $SD = 1$)

prior to analysis in Program PRESENCE. My 22 a priori candidate models included ≤ 2 covariates each and were ranked using Akaike's Information Criterion (AICc; Burnham and Anderson 2002) to determine which covariates most influenced detection.

TRAINING OF DETECTION DOGS

Working Dogs for Conservation (WDC) trained detection dogs following procedures similar to those used in detection of narcotics and explosives (see Smith et al. 2003, Wasser et al. 2004). Dogs are chosen for training that have a strong object orientation and play drive, making them highly motivated to work for a play object such as a ball. Dogs are trained to associate the scent of a target organism or scat with a play object, and then learn to actively search for the target scent. Dogs also are trained to sit and stay at the source of a target scent when they are able to pinpoint its location (i.e., point nose at scat or live animal in a container) or come as close to the odor as possible (i.e., put nose in entrance of a burrow occupied by a target organism). This trained behavior becomes the alert that notifies a dog handler that the source of a target scent has been located. After performing an alert, if the handler is able to confirm presence of a target (e.g., a radiomarked individual is confirmed in the area), the dog receives a play object as a reward. Although the trained alert is the behavior preferred by handlers to indicate presence of a target scent, a handler also may observe a detection dog's body language (Rebmann et al. 2000, SWGDOG 2008). Detection dogs demonstrate natural changes in behavior that reflect excitement upon encountering a target scent—movement quickens, searching intensifies, and often tail wagging begins (Rebmann et al. 2000, SWGDOG 2008). Because these behavioral changes are not trained responses, require interpretation by a handler, and vary by dog (Rebmann et al. 2000, SWGDOG 2008), these “on-scent” behaviors are not considered an ideal means of

communication between detection dog and handler (Cablk and Heaton 2006). However, on-scent behaviors may be helpful in assessing presence of a target organism when a dog is not able to get directly to the source of a scent (e.g., a target organism has left the survey area, but its residual scent lingers).

In 2008, WDC trained a detection dog to recognize and discriminate between scent of scats from Franklin's ground squirrels and thirteen-lined ground squirrels. We ran trials in which scat samples from both Franklin's ground squirrels and thirteen-lined ground squirrels were placed in grass. The dog ignored 89% of scat samples from thirteen-lined ground squirrels ($n = 244$ exposures) and alerted to 100% of scat samples from Franklin's ground squirrels ($n = 82$ exposures). However, when practice surveys were conducted in a grassland occupied by Franklin's ground squirrels (Barnhart Prairie Nature Preserve, Champaign, IL), the detection dog did not alert, indicating the dog team was unlikely to encounter ground squirrel scat above ground under natural conditions. Thus, in 2009 we refocused training on detection of live Franklin's ground squirrels and burrows.

In 2009, WDC trained 2 detection dogs with experience in live animal detection to detect live Franklin's ground squirrels. We conducted training in two phases. First, we exposed detection dogs to Franklin's ground squirrels placed in polyvinyl chloride (PVC) tubes (10.2 cm diameter; 0.3 or 2-3 m length) capped with PVC floor strainers, which allowed dogs to smell squirrels without seeing them (Figure 2.1a). During the first 2 days of training, we placed squirrels in short PVC tubes (0.3 m length) above ground in tall grass so dogs would encounter squirrel scent while walking through vegetation similar to that in actual surveys. Next, to simulate encounters with squirrels in burrow-like conditions, we placed squirrels in short tubes in holes flush with the ground. Beginning on the third day of training, to expose detection dogs to

lower levels of scent expected under natural conditions, we placed squirrels in long PVC tubes (2-3 m length) and constrained squirrel movement to the 0.3 m furthest from the detection dog, added fresh soil to the end of the tube nearest the detection dog, and added multiple 90-degree turns using PVC elbows. Given the length of the long tubes, we could not place them in holes and instead placed them above ground in tall grass (Figure 2.1b). During all training, handlers walked detection dogs along a transect exposing dogs to 4-5 PVC tubes placed 3 m apart and recorded when and where dogs alerted. Some PVC tubes held Franklin's ground squirrels or thirteen-lined ground squirrels, and others were empty controls. Handlers rewarded dogs with a play object when dogs performed alerts at PVC tubes holding Franklin's ground squirrels. To prevent scent contamination, we were careful to keep PVC tubes that held Franklin's ground squirrels separated from PVC tubes that remained empty or held thirteen-lined ground squirrels. Throughout training, we exposed detection dogs to Franklin's ground squirrel scats placed on the soil surface in grass. Handlers walked detection dogs along a transect exposing dogs to 4-5 Franklin's ground squirrel scats placed 3 m apart and recorded when and where dogs alerted. Overall, the detection dogs received 52 exposures to Franklin's ground squirrels in short PVC tubes, 246 exposures to Franklin's ground squirrels in long PVC tubes, 59 exposures to Franklin's ground squirrel scat, and 9 exposures to thirteen-lined ground squirrels in long PVC tubes.

Our second phase of training consisted of placing radiotransmitter collars (model M1540, Advanced Telemetry Systems, Isanti, Minnesota) on 6 Franklin's ground squirrels and exposing the detection dogs to burrows that housed these squirrels. Each exposure consisted of a handler walking a detection dog past a burrow with a radiomarked Franklin's ground squirrel, beginning 3 m away from the burrow and getting successively closer, if needed, until the dog was able to

sniff the burrow entrance directly, and recording whether the dog alerted. In three cases, after waiting ≥ 30 min, we re-exposed a dog to a burrow at which it did not alert if the other dog alerted at the same burrow, demonstrating scent was available. During the last 4 days of training, the dogs received 44 exposures to burrows containing radiomarked squirrels. We conducted all training at the Barnhart Prairie Nature Preserve.

I used logistic regression analysis (SYSTAT[®] 12 2007) to determine if detection of Franklin's ground squirrels (alert = 1, no alert = 0) differed between the 2 detection dogs or depended on exposure type (scat, short PVC tubes, long PVC tubes, and radiomarked squirrels in natural burrows) in which scat was set as the reference category. I evaluated an additive model without interactions, and contrasted groups using an odds ratio (OR).

OCCUPANCY SURVEYS WITH DETECTION DOGS

After 8 days of training and initial trials, we conducted presence-absence surveys using dog teams at 40 of the 62 sites surveyed via livetrapping. For most sites (33 of 40), we conducted dog team surveys before live-trapping surveys and thus did not know beforehand how many sites had squirrels present in 2009; dog handlers did not know if squirrels were present at the time of dog surveys or in previous years at any sites. The two survey methods were never used simultaneously at a site. Twenty sites were surveyed by a single dog team, and 20 sites were surveyed twice with one independent survey by each dog team. To minimize time in the field, the 2 dog teams worked simultaneously, but at separate sites. All dog surveys were conducted during the morning (0700 – 1100 h). A survey consisted of a handler walking a detection dog along each of 2 90-m trapping transects twice, once in each direction (traps were not present), covering the area extending 10 m in all directions from each transect. Each handler

recorded times and locations of trained alert responses by dogs. Handlers also recorded and interpreted a change of behavior in dogs to identify sites where dogs seemed to recognize scent of Franklin's ground squirrels but were unable to pinpoint origin of scent and thus alert. Handlers noted the potential for Franklin's ground squirrel presence if dogs showed at least one change of behavior consistent with detecting scent of Franklin's ground squirrels (i.e., quickened pace, quickened sniffing, wagging tail) and encountered no other potential triggers for excitement (i.e., rabbit, carnivore scat).

Because occupancy modeling generally assumes a species is never falsely detected at a site (MacKenzie et al. 2006), and false positives were possible for surveys with dog teams, I did not use occupancy modeling to estimate detection rates for dog surveys. Although an occupancy model was developed to allow for false positives (Royle and Link 2006), the procedure does not account for biases in detection probabilities introduced by use of multiple survey methods (Fitzpatrick et al. 2009). Instead, because cumulative probability of detection was close to 1.0 after 4 days of trapping (0.97, see results), I treated presense-absence results from trapping as the "truth" to which I compared data collected by dog teams. These comparisons allowed me to calculate approximate rates of detection and number of false positives for surveys conducted by dog teams.

SURVEY COST

I tracked starting costs (i.e., live traps, training supplies, salary during training, room and board, and mileage between WDC headquarters and a training or study site) and survey costs (i.e., salary during surveys; room and board; mileage to, from, and among study sites) while using livetrapping with 2 technicians (2007-2009) and 2 dog teams (2008-2009) to survey for

Franklin's ground squirrels. At each site, I conducted 4 consecutive days of livetrapping surveys. Half of sites received 1 dog team survey and half received 2 consecutive surveys by independent dog teams. I used this information to estimate and compare cost of surveys between dog teams and livetrapping. All cost estimates for surveys using dog teams were based on contracting dog teams through WDC.

RESULTS

DETECTION BY DOGS DURING TRAINING

The model including detection dog identity (dog #1 or dog #2) and exposure type as covariates for detection of Franklin's ground squirrels had a better fit (Nagelkerke's $R^2 = 0.30$) than the intercept-only model (Likelihood Ratio Test, $\chi^2_4 = 102.68$, $P < 0.001$). Detection rate of Franklin's ground squirrels during training did not differ between the two dogs (OR = 1.50, 95% CI = 0.95-2.34; Figure 2.2). The odds of dogs detecting squirrels in short PVC tubes did not differ from the odds of detecting scat on the soil surface (OR = 2.98, 95% CI = 0.30-29.53). However, detection dogs were less likely to detect either squirrels in long PVC tubes (OR = 0.05, 95% CI = 0.02-0.18) or radiomarked individuals in natural burrows (OR = 0.05, 95% CI = 0.01-0.17) than surface scat (Figure 2.2). Detection dogs falsely alerted in 2 of the 9 (22%) exposures to thirteen-lined ground squirrels in long PVC tubes.

SURVEY EFFECTIVENESS OF LIVETRAPPING AND DOG TEAMS

For occupancy surveys based on livetrapping, the detection model including daily precipitation as a covariate and the intercept-only model received the most support (Table 2.1). Three 2-covariate detection models also were competitive ($\Delta AIC_c \leq 2$); however, these models

had log-likelihood values similar to the top model (Table 2.1), which suggests little support for the added complexity (Burnham and Anderson 2002). Daily precipitation negatively affected detection rate ($\beta = -0.23$, $SE = 0.17$). Estimates of per-survey (i.e., daily) detection rate (p) for each site ranged from 0.30 ($SE = 0.20$) to 0.62 ($SE = 0.04$) with a median value of 0.61 ($SE = 0.04$), indicating I typically had a 61% chance of capturing a Franklin's ground squirrel with one day of livetrapping if the species was present. Similarly, p was estimated as 0.60 ($SE = 0.04$) for the intercept-only model. I estimated the cumulative probability of detecting a Franklin's ground squirrel at least once over 4 trapping surveys using the equation $1-(1-p)^k$, in which p is the probability of detecting a species after a single survey and k is the number of surveys (MacKenzie 2005). Cumulative probability of detection at a site was 0.97 based on the intercept-only model. Six sites received enough precipitation in 2009 to reduce their cumulative probability of detecting a Franklin's ground squirrel after 4 days of livetrapping, but the reduction was only from 0.97 to 0.94. Because Franklin's ground squirrels were easily identified once captured, the probability of producing a false positive with livetrapping was 0.

During 4 days of livetrapping at each site from 20 May – 16 July 2009, I captured Franklin's ground squirrels at 10 of 40 study sites surveyed by dog teams. I used these trapping results as the benchmark for evaluating effectiveness of surveys by detection dogs. For dog surveys, alerts or on-scent dog behavior suggesting presence of Franklin's ground squirrels were defined as “true positives” on sites where the species was captured in 2009 and as “false positives” on sites where the species was not captured in 2009. Mean time required to survey a site with a dog team was 21 min ($n = 60$ surveys, $SE = 0.75$, min = 8 min, max = 33 min). Detection rates of single dog teams averaged 36% when based on alerts, but increased to an average of 58% when based on alerts plus on-scent dog behavior (Table 2.2). Additionally, on

sites surveyed by both dog teams, probability of detection based on data from both teams combined increased from 67% when based on alerts to 83% when based on alerts plus on-scent dog behavior (Table 2.2). The rate of false positives for single dog teams varied from 17-21% when based on alerts, but increased to 17-43% when based on alerts plus on-scent dog behavior, and to 35% when based on alerts plus on-scent dog behavior with both teams combined (Table 2.2).

SURVEY COST

Starting costs for livetrapping surveys included salary for 2 livetrapping technicians during 4 days of pre-survey training, the cost of 140 live traps, and trapping supplies such as bait and handling gear. Given my experimental design with 20 traps set at each site, 2 technicians could set and check traps at ≤ 7 sites (140 traps set or checked within 2 hr) per day when sites were within a 5-km radius. Starting costs for dog team surveys included 10 days of dog training; mileage for 4 days of travel (roundtrip) between Montana and training site in Illinois; per diem and lodging during days of travel, training, and rest; and training supplies such as PVC tubes. Total starting costs for livetrapping with 2 technicians (\$5,224) was less than for 2 dogs trained in Champaign, IL (\$7,774; Table 2.3).

When 2 dog teams independently surveyed the same sites and I based analyses on alerts plus on-scent dog behavior, the probability of detecting Franklin's ground squirrel presence ($p = 0.83$) was comparable to the probability of detection after 2 consecutive days of livetrapping ($p = 0.84$). Therefore, even though my original survey protocol for 2007 – 2009 called for 4 daily livetrapping surveys (total cost over 40 sites = \$12,769), I considered the most straightforward comparison to be costs of 2 independent dog team surveys to those of 2 daily livetrapping

surveys. Total survey cost for 2 consecutive days of livetrapping conducted by 2 technicians at 40 sites (\$7,045) was less than total cost for 2 consecutive surveys by independent dog teams at 40 sites (\$8,003; Table 2.3). Total survey cost for 2 consecutive days of livetrapping conducted by 2 technicians over my entire 62 sites (\$9,907) was less than the estimated cost of 2 consecutive surveys by independent dog teams (\$11,156), but would have taken about twice as long (18 versus 9 days of surveys).

DISCUSSION

In contrast to my prediction, the probability of detecting presence of Franklin's ground squirrels during a single dog team survey (36% based on alerts, 58% based on alerts plus on-scent behavior) was not greater than during a single daily livetrapping survey (median = 61%). Detection of Franklin's ground squirrels by a single dog team survey was lower than that reported for detection of scat from carnivores such as black bears (86-87%) and fishers (84-95%), but greater than that reported for detection of bobcat scat (13-40%; Long et al. 2007*a, b*) when I based presence on alerts plus on-scent behavior, rather than solely alerts. However, when 2 dog teams independently surveyed the same sites, the probability of detecting presence (83% based on alerts plus on-scent behavior) was comparable to the probability of detection after 2 daily livetrapping surveys (84%), as well as to detection rates of carnivore scat (Long et al. 2007*a, b*) and burrowing animals such as desert tortoises (70%; Nussear et al. 2008) and black-footed ferrets (79-86%; Reindl-Thompson et al. 2006). As predicted, cost of a single dog team survey was higher than cost of a livetrapping survey, however, dog teams were not so efficient as to make dog-handler surveys more cost-effective than livetrapping surveys for my 40 study sites.

Costs described herein were specific to my study, and thus should be considered only approximations. For example, travel costs between WDC headquarters in Montana and other study sites will be different. My technicians were university students paid \$10/hr; technicians employed by professional agencies may receive higher salaries. Overall, I did not consider the difference in cost for the two survey methods to be substantial. A major difference, however, was the amount of time required to complete surveys. Whereas livetrapping surveys typically require repeated visits (e.g., 2-3 times per day) to study sites over several days, multiple, independent surveys of a site by dog teams can easily be conducted in a single day. For species such as Franklin's ground squirrel that are only active above ground for a limited time each year, time constraints can be critical if surveys of many sites over a large geographic area are needed. Following my protocols (2 daily livetrapping surveys, 2 surveys by dog-handler teams), the same number of technicians could survey about twice as many sites using detection dogs as by livetrapping. If livetrapping protocols were extended to 3 or 4 days, the difference is even greater. While detection dogs minimize time invested in surveys, they are likely to require a longer training period than technicians (Table 2.3). Thus, researchers might experience a net gain in time only when conducting a large number of surveys.

Confirming presence of a cryptic species such as Franklin's ground squirrel is not always feasible, making it possible to erroneously reward false positives, which can confuse detection dogs and lead to increased false positive alerts. Several factors could have contributed to dogs behaving as if they detected scent at sites where squirrels were not captured. First, dog behavior suggested presence of Franklin's ground squirrels on 4 sites at which squirrels were not captured in 2009, but were captured in either 2007 or 2008. Site turnover (i.e., local extinctions and colonizations) may be frequent in some areas and is likely influenced by habitat quality and the

level of connectivity between sites (Hanski and Gaggiotti 2004). I do not know how long scent may persist at a site after squirrels are no longer present, particularly in abandoned burrows.

Second, I recorded only single captures of a Franklin's ground squirrel at 6 of my 62 study sites in 2009, suggesting sites may be visited by transient squirrels without burrows on site. Because I constrained the search area at each site, dogs might have responded to residual scent from a squirrel that visited a site from a nearby area prior to the dog team survey, but not during the livetrapping survey. Franklin's ground squirrels on a 152-ha Waterfowl Production Area in North Dakota had a mean home range size >8 ha and a mean daily travel distance >100 m (Choromanski-Norris et al. 1989). Thus, squirrels willing to traverse inhospitable habitat could easily visit a study site and return to a home burrow in 1 day. However, because dogs are trained to alert only after finding the exact location of a scent, dogs sometimes may have been unable to alert to diffuse residual scent left in abandoned burrows or by transient squirrels. Both the ability of detection dogs to detect residual scent after a target species is gone and the inability to alert to diffuse scent can confound comparisons between detection dogs and other methods that detect species presence based on evidence of current occupancy such as captures, scats, or other sign (Long et al. 2007a). Whereas detection dog alerts at abandoned or visited sites will inflate estimates of current occupancy relative to estimates from methods such as livetrapping, information on abandoned or visited sites could be useful in indicating potential habitat where recolonization is possible. If potentially suitable habitat is available, researchers interested only in current occupancy should consider increasing the size of study sites relative to movement distances of study organisms to decrease the likelihood of false positives during detection dog surveys.

The burrowing habits, preference for dense vegetation, small body size, and small scat size of Franklin's ground squirrels likely provided detection dogs with a weak scent in either quantity or distance the scent can travel, increasing the likelihood of false negatives. By using multiple types of exposures to target scent, we tried to train detection dogs to alert to the detection of Franklin's ground squirrels when scent was weak. Use of long PVC tubes with elbows during training seemed effective in providing a low level of scent similar to that provided by a radiomarked squirrel in a natural burrow. Although detection dogs were excellent at detecting ground squirrels in short tubes and scat on the soil surface, they alerted to squirrels in long PVC tubes or natural burrows in only 29-60% of exposures (Figure 2.2). Given the weak scent and poor airflow conditions provided by Franklin's ground squirrels in burrows, detection rates for the species by dog teams might not improve beyond rates observed in this study, even with more training. We attempted to compensate for potentially weak scent cues by conducting dog team surveys slowly within constrained areas, as slow searches permit longer exposures to odor and better discrimination accuracy for weak scents (Rinberg et al. 2006). Gsell et al. (2010) found detection dogs could survey 5-6.7 ha/hr while searching for released laboratory rats and mice in a rodent-free forest sanctuary, but our detailed searches for Franklin's ground squirrels in dense grassland habitat covered only slightly more than 1 ha/hr. Further mitigation of this challenge might include conducting surveys earlier in the season when vegetation is shorter, which might allow better airflow for scent, as well as observation of burrow entrances.

Interpreting on-scent dog behavior as a potential indicator of species presence could reduce false negatives; of 9 sites where dogs showed intensified interest but did not alert, 3 sites had captures of Franklin's ground squirrels in 2009 and 2 additional sites had captures in 2007-2008. Interpreting on-scent behavior also resulted in an increase in false positives. In fields such

as pest management, detection dogs meet the minimum standard of acceptability only when false positive rates are $\leq 10\%$ (Brooks et al. 2003). However, I concur with Goodwin et al. (2010) that minimizing false negatives, and perhaps accepting a higher rate of false positives, should be a priority when conducting initial status or distribution surveys for both invasive and rare and cryptic species.

For projects covering large spatial and temporal scales (e.g., mapping geographic distribution, monitoring spatial or temporal trends in occupancy), I propose a two-stage strategy for maximizing the number of sites that can be surveyed in a limited time while minimizing false positives. First, researchers should determine how many dog team surveys are necessary to acquire an acceptably high cumulative detection rate for their target species, and then conduct that number of dog team surveys at each site. Livetrapping is later conducted only on sites where on-scent behavior by detection dogs suggested presence of a target species. By conducting initial surveys with dog teams, sites unlikely to contain a target species can be eliminated from a study quickly and efficiently. Initial surveys by dog teams also can be flexible: with little extra cost, the area sampled by dog teams can be increased at sites where dog behavior suggests possible presence, but no alert is triggered, thus allowing dogs the opportunity to locate the source of scent when outside the initial survey area. Although combining methods will be more costly than using a single method, using dog-handler surveys to winnow prospective sites can substantially decrease the number of sites surveyed by livetrapping, or identify subareas where trapping should be conducted within large sites. Following dog team surveys with a second survey method (i.e., livetrapping) allows for confirmation of a target species and reduction of false positives (Reindl-Thompson et al. 2006, Dematteo et al. 2009), which is important for an accurate status assessment of rare species. If a large number of sites are surveyed to monitor

temporal trends in occupancy or conduct a general status assessment, livetrapping at a subsample of the sites where dog behavior indicated presence can be used to estimate the false-positive rate, and that estimate applied to untrapped sites. Livetrapping surveys can proceed until a desired detection rate is met (e.g., 4 days for a detection rate of 97% for Franklin's ground squirrels), and because the number of study sites requiring livetrapping has been reduced, detection rate can be maximized while reducing time, labor, and costs.

MANAGEMENT IMPLICATIONS

Use of detection dogs in surveys for mammals has been applied primarily to carnivores that leave large scat available for detection (MacKay et al. 2008). My results indicate detection dogs also can be effectively used for sampling small, burrowing, omnivorous species that leave less obvious sign above ground. Detection dogs were capable of distinguishing closely related species during surveys. This discrimination is not surprising given studies indicating detection dogs can distinguish individuals based on scat (Kerley and Salkina 2007, Wasser et al. 2009). The main advantage of using detection dogs in my study was that about twice as many sites could be surveyed in a field season than via standard livetrapping protocols at only a modestly greater cost. Detection dog surveys are rapid (mean = 21 min in this study) and should not cause significant disruptions in squirrel behavior or increase attraction of predators more than surveys conducted by humans alone (Heaton et al. 2008). Use of detection dogs also reduces stress on target species resulting from trapping and handling, and avoids restraining lactating females in traps away from their offspring. However, sampling with only detection dogs precludes collection of mark-recapture data, or tissue, blood, and parasite samples. Survey objectives, study design, and study area (i.e., climate, vegetation, and topography) will determine if

detection dogs can provide an appropriate and effective sampling method for a study (Long et al. 2007a, b). I suggest a two-stage survey strategy that integrates detection dog surveys with follow-up livetrapping can be effectively used in large-scale surveys of Franklin's ground squirrels to maximize the number of sites surveyed while minimizing bias due to false positives, and I think this strategy can be applied to a wider array of rare and cryptic species.

ACKNOWLEDGMENTS

I thank N. Karniski, J. Nachel, and H. Pioch for their assistance in the field and detection dogs, Wicket and Camas, for their contributions to this project. I am also grateful to the Barnharts for allowing me to use their property as a training ground. I thank reviewers for valuable comments on this manuscript. This project was funded by the Illinois Department of Natural Resources through the Federal Aid in Wildlife Restoration Program (Project W-152-R), University of Illinois, Illinois Natural History Survey, American Society of Mammalogists, and American Museum of Natural History through a Theodore Roosevelt Memorial Fund award.

REFERENCES

- ARNETT, E. B. 2006. A preliminary evaluation on the use of dogs to recover bat fatalities at wind energy facilities. *Wildlife Society Bulletin* 34:1440-1445.
- BROOKS, S. E., F. M. OI, AND P. G. KOEHLER. 2003. Ability of canine termite detectors to locate live termites and discriminate them from non-termite material. *Journal of Economic Entomology* 96:1259-1266.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CABLK, M. E., AND J. S. HEATON. 2006. Accuracy and reliability of dogs in surveying for desert tortoise (*Gopherus agassizii*). *Ecological Applications* 16:1926-1935.
- CHORMANSKI-NORRIS, J., E. K. FRITZELL, AND A. B. SARGEANT. 1989. Movements and habitat use of Franklin's ground squirrels in duck-nesting habitat. *Journal of Wildlife Management* 53:324-331.
- DEMATTEO, K. E., M. A. RINAS, M. M. SEDE, B. DAVENPORT, C. F. ARGÜELLES, K. LOVETT, AND P. G. PARKER. 2009. Detection dogs: an effective technique for bush dog surveys. *Journal of Wildlife Management* 73:1436-1440.
- DENVER, M., J. PEREZ, AND B. E. AGUIRRE. 2007. Local search and rescue teams in the United States. *Disaster Prevention and Management* 16:503-512.
- FITZPATRICK, M. C., E. L. PREISSER, A. M. ELLISON, AND J. S. ELKINTON. 2009. Observer bias and the detection of low-density populations. *Ecological Applications* 19:1673-1679.
- GASTON, K. J. 1994. *Rarity*. Chapman and Hall, London, United Kingdom.

- GOODWIN, K. M., R. E. ENGEL, AND D. K. WEAVER. 2010. Trained dogs outperform human surveyors in the detection of rare spotted knapweed (*Centaurea stoebe*). *Invasive Plant Science and Management* 3:113-121.
- GSELL, A., J. INNES, P. DE MONCHY, AND D. BRUNTON. 2010. The success of trained dogs to locate sparse rodents in pest-free sanctuaries. *Wildlife Research* 37:39-46.
- GUTZWILLER, K. J. 1990. Minimizing dog-induced biases in game bird research. *Wildlife Society Bulletin* 18:351-356.
- HANSKI, I. A., AND O. E. GAGGIOTTI. 2004. Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, Amsterdam, Netherlands.
- HARRISON, R. L. 2006. A comparison of survey methods for detecting bobcats. *Wildlife Society Bulletin* 34:548-552.
- HEATON, J. S., M. E. CABLK, K. E. NUSSEAR, T. C. ESQUE, P. A. MEDICA, J. C. SAGEBIEL, AND S. S. FRANCIS. 2008. Comparisons of effects of humans versus wildlife detector dogs. *The Southwestern Naturalist* 53:472-479.
- HOFMANN, J. E. 2008. Field manual of Illinois mammals. Illinois Natural History Survey, Champaign, Illinois.
- HOMAN, H. J., G. LINZ, AND B. D. PEER. 2001. Dogs increase recovery of passerine carcasses in dense vegetation. *Wildlife Society Bulletin* 29:292-296.
- HUEBSCHMAN, J. J. 2003. A conservation assessment of Franklin's ground squirrel (*Spermophilus franklinii* Sabine 1822): input from natural history, morphology and genetics. Dissertation, University of Nebraska, Lincoln.
- HURT, A., AND D. A. SMITH. 2009. Conservation dogs. Pp 175-194 in *Canine ergonomics: the science of working dogs* (W. S. Helton, ed.). CRC Press, Boca Raton, Florida.

- JOHNSON, S. A., AND J. CHOROMANSKI-NORRIS. 1992. Reduction in the eastern limit of the range of the Franklin's ground squirrel (*Spermophilus franklinii*). American Midland Naturalist 128:325-331.
- KERLEY, L. L., AND G. P. SALKINA. 2007. Using scent-matching dogs to identify individual Amur tigers from scats. Journal of Wildlife Management 71:1349-1356.
- LONG, R. A., T. M. DONOVAN, P. MACKAY, J. S. BUZAS, AND W. J. ZIELINSKI. 2007a. Comparing detection dogs, cameras, and hair snares for surveying carnivores. Journal of Wildlife Management 71:2018-2025.
- LONG, R. A., T. M. DONOVAN, P. MACKAY, W. J. ZIELINSKI, J. S. BUZAS. 2007b. Effectiveness of scat detection dogs for detecting forest carnivores. Journal of Wildlife Management 71:2007-2017.
- MACKAY, P., D. A. SMITH, R. A. LONG, AND M. PARKER. 2008. Scat detection dogs. Pp. 183-222 in Noninvasive survey methods for carnivores (R. A. Long, P. MacKay, W. Zielinski, and J. C. Ray, eds.). Island Press, Washinton, D.C.
- MACKENZIE, D. I. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69:849-860.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, Amsterdam, Netherlands.
- MARTIN, J. M., E. J. HESKE, AND J. E. HOFMANN. 2003. Franklin's ground squirrel (*Spermophilus franklinii*) in Illinois: A declining prairie mammal? American Midland Naturalist 150:130-138.

- MARTIN, J. M., AND E. J. HESKE. 2004. Juvenile dispersal of Franklin's ground squirrel (*Spermophilus franklinii*) from a prairie "island". American Midland Naturalist 153:444-449.
- NUSSEAR, K. E., T. C. ESQUE, J. S. HEATON, M. E. CABLK, K. K. DRAKE, C. VALENTIN, J. L. YEE, AND P. A. MEDICA. 2008. Are wildlife detector dogs or people better at finding desert tortoises (*Gopherus agassizii*)? Herpetological Conservation and Biology 3:103-115.
- REBMANN, A., E. DAVID, AND M. H. SORG. 2000. Cadaver dog handbook: forensic training and tactics for the recovery of human remains. CRC Press LLC, Boca Raton, Florida.
- REINDL-THOMPSON, S. A., J. A. SHIVIK, A. WHITELAW, A. HURT, AND K. F. HIGGINS. 2006. Efficacy of scent dogs in detecting black-footed ferrets at a reintroduction site in North Dakota. Wildlife Society Bulletin 34:1435-1439.
- RINBERG, D. A. KOULAKOV, AND A. GELPERIN. 2006. Speed-accuracy tradeoff in olfaction. Neuron 51:351-358.
- ROBERTSON, H. A., AND J. R. FRASER. 2009. Use of trained dogs to determine the age structure and conservation status of kiwi *Apteryx* spp. populations. Bird Conservation International 19:121-129.
- ROLLAND, R. M., P. K. HAMILTON, S. D. KRAUS, B. DAVENPORT, R. M. GILLET, AND S. M. WASSER. 2006. Faecal sampling using detection dogs to study reproduction and health in North Atlantic right whales (*Eubalaena glacialis*). Journal of Cetacean Research and Management 8:121-125.
- ROYLE, J. A., AND W. A. LINK. 2006. Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87:835-841.

SCIENTIFIC WORKING GROUP ON DOGS AND ORTHOGONAL DETECTION GUIDELINES [SWGDOG].

2008. Selection of Serviceable Dogs, Forensic Science Communications.

<<http://www.ncjrs.gov/App/Publications/abstract.aspx?ID=247086>>. Accessed 28 Feb 2010.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN

SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of

Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.

SLABBERT, J. M., AND J. S. J. ODENDAAL. 1999. Early prediction of adult police dog efficiency- a longitudinal study. *Applied Animal Behaviour Science* 64:269-288.

SMITH, D. A., K. RALLS, A. HURT, B. ADAMS, M. PARKER, B. DAVENPORT, M. C. SMITH, AND J. E.

MALDONADO. 2003. Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes (*Vulpes macrotis mutica*). *Animal Conservation* 6:339-346.

WASSER, S. K., B. DAVENPORT, E. R. RAMAGE, K. E. HUNT, M. PARKER, C. CLARKE, AND G.

STENHOUSE. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. *Canadian Journal of Zoology* 82:475-492.

WASSER, S. K., SMITH, H., MADDEN, L., MARKS, N., AND C. VYNNE. 2009. Scent-matching dogs determine number of unique individuals from scat. *Journal of Wildlife Management*

73:1233-1240.

TABLES AND FIGURES

Table 2.1 Detection models for Franklin’s ground squirrels ranked using Akaike’s Information Criterion (AIC_c). Detection models were developed using livetrapping data from 62 study sites throughout Midwestern U.S., 2007 – 2009. Occupancy [Ψ], colonization [γ], and extinction [ϵ] are held constant. Detection covariates included year, Julian date, day 1-4 of trap session, maximum and minimum daily temperature, and daily precipitation. Information for each model includes AIC difference (Δ AIC_c; difference between model AIC_c and lowest AIC_c), AIC weight (ω ; weight of evidence in favor of a given model), number of estimable parameters (K), and -2loglikelihood (-2Log[L])

Model	Δ AIC _c	ω	K	-2Log(L)
$\psi(.)\gamma(.)\epsilon(.)p$ (Precipitation)	0.00	0.195	5	445.43
$\psi(.)\gamma(.)\epsilon(.)p$ (.)	0.67	0.134	4	448.10
$\psi(.)\gamma(.)\epsilon(.)p$ (Precipitation + MaxTemp)	1.61	0.087	6	445.04
$\psi(.)\gamma(.)\epsilon(.)p$ (Precipitation + MinTemp)	1.72	0.083	6	445.15
$\psi(.)\gamma(.)\epsilon(.)p$ (Precipitation + Julian)	2.00	0.072	6	445.43

Table 2.2 Numbers of true and false positives based on alerts and on-scent dog behavior during detection dog surveys for Franklin’s ground squirrels in Midwestern U.S., 2009. Designations of outcomes as true or false are based on where captures of Franklin’s ground squirrels occurred during livetrapping surveys. Twenty sites were surveyed only by one detection dog-handler team (10 sites each), and 20 sites were surveyed twice with one independent survey by each dog-handler team. Rates are shown for dog-handler teams both separately and combined where sites were surveyed twice

Team	No. of sites	No. sites with captures	Positives	Alerts No. (%)	Behavior No. (%)
1	30	6	True	4 (67)	4 (67)
			False	5 (21)	8 (33)
2	30	10	True	2 (20)	5 (50)
			False	4 (20)	7 (35)
Combined	20	6	True	4 (67)	5 (83)
			False	3 (21)	7 (50)

Table 2.3 Starting (A) and survey (B) costs for livetrapping versus detection dogs used to determine occupancy by Franklin's ground squirrels on 40 study sites (2 parallel 90 m transects set 10 m apart) in Midwestern U.S., 2009. Livetrapping was conducted by 2 technicians for 2 consecutive days and detection dog surveys were run using 1-2 independent dog teams. Information for each cost also includes the number of days over which cost was accrued

(A) Starting method	Starting Costs	Cost per unit	No. Days	Total cost
Livetrapping	Training in IL	\$80/day per technician	4	\$640
	Lodging		4	\$0
	Per Diem		4	\$0
	Supplies	\$32.60/trap x 140 traps		\$4,564
	Supplies	Bait, handling gear, etc.		\$20
	TOTAL		4	\$5,224
Dog teams	Training in IL ^a	\$200/day per team	10	\$2,000
	Lodging	\$70/day per handler	18	\$2,520
	Per Diem	\$39/day per handler	18	\$1,404
	Travel to IL (roundtrip)	\$0.55/mile x 3000 miles	4	\$1,650
	Supplies	PVC tubes, etc.		\$200
	TOTAL		18 ^b	\$7,774

(B) Survey method	Survey costs	Cost per unit	No. Days	Total cost
Livetrapping	Salary	\$80/day per technician	12	\$1,920
	Lodging	\$70/day per technician	14	\$1,960
	Per diem	\$39/day per technician	14	\$1,092
	Travel to/from study sites	\$0.55/mile x 1,500 miles	2	\$825
	Travel among study sites	\$0.55/mile x 60 miles/day x 3	12	\$1,188
	Supplies	Bait, handling gear, etc.		\$60
	TOTAL		14	\$7,045
Dog teams	Salary ^a	\$400/day per team	6	\$4,800
	Lodging	\$70/day per handler	10	\$1,400
	Per diem	\$39/day per handler	10	\$780
	Travel to/from study sites	\$0.55/mile x 1,500 miles	2	\$825
	Travel among study sites	\$0.55/mile x 60 miles/day	6	\$198
	Supplies			\$0
	TOTAL		10 ^b	\$8,003

^aSalary covers veterinarian care, food, and insurance for detection dogs.

^bDetection dog-handler teams required 2 days of rest for every 5 days of work.

Figure 2.1 Photographs of polyvinyl chloride (PVC) tubes used to restrain Franklin's ground squirrels during training. (A) Short PVC tube (10.16 cm diameter; 0.3 m length) capped with PVC floor strainers. (B) Long PVC tube (10.16 cm diameter, 2-3 m length) with multiple 90 degree turns created using PVC elbows

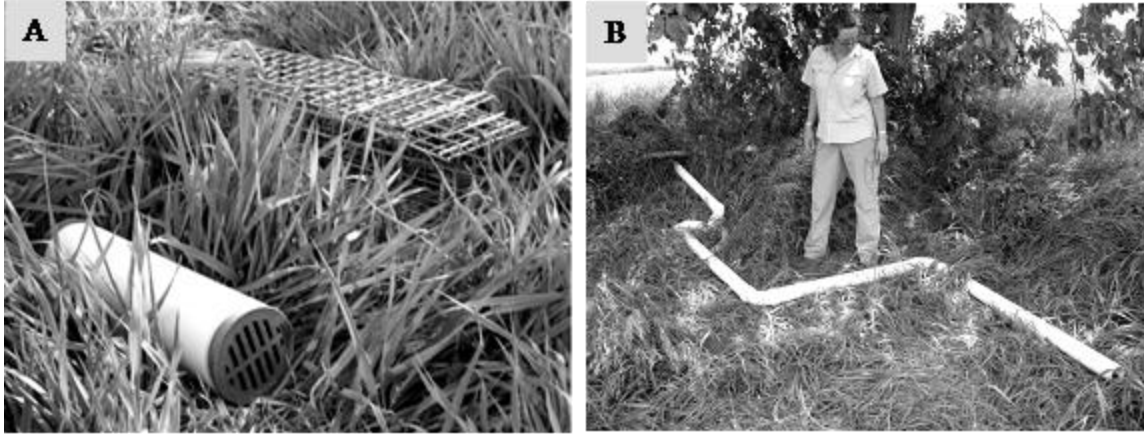
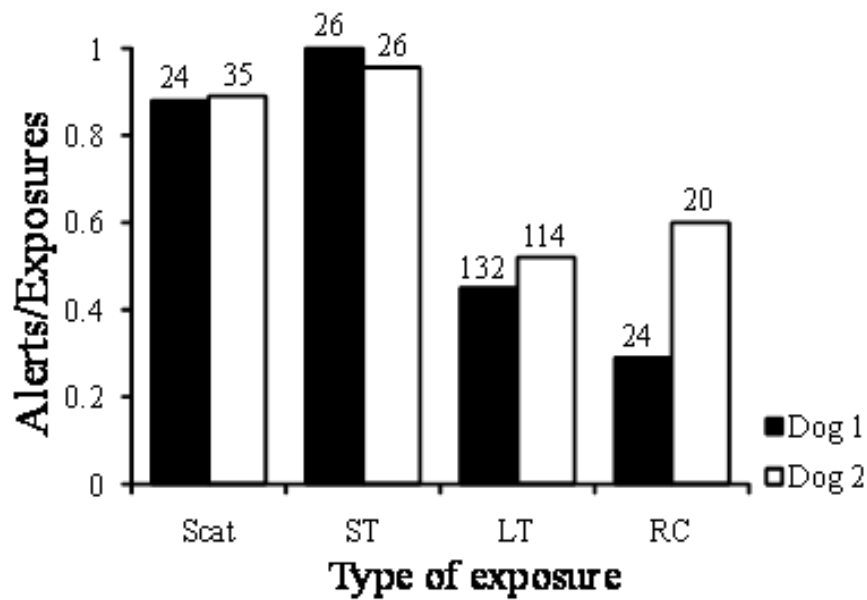


Figure 2.2 Proportion of exposures receiving alerts from Dog 1 and Dog 2 during training. Types of exposures included Franklin's ground squirrel scat set in grass (Scat), Franklin's ground squirrels placed in short polyvinyl chloride (PVC) tubes set in tall grass or in holes flush with the ground (ST), Franklin's ground squirrels placed in long PVC tubes set in tall grass (LT), and radio-collared squirrels in burrows (RC). Numbers above bars indicate sample sizes for each dog-exposure type combination



CHAPTER 3

GAP-CROSSING DECISIONS BY FRANKLIN'S GROUND SQUIRREL IN AGRICULTURAL LANDSCAPES

ABSTRACT

In the Midwestern U.S., grassland habitat is fragmented by row-crop agriculture and urbanization. In spring and early summer, grassland animals facing a decision to either enter a fallow crop field or detour around it likely balance trade-offs between predation risk and travel costs, similar to forest animals encountering a clearcut. I tested if Franklin's ground squirrel (*Poliocitellus franklinii*), a grassland mammal, based gap-crossing decisions on lengths of alternate movement routes or on individual energetic constraints by translocating radiocollared adult squirrels across crop fields and tracking routes home. Giving-up-densities indicated *P. franklinii* perceived a higher risk of predation in crop fields than in grass, but travel speed, calculated using telemetry locations, was not strongly adjusted to compensate for risk when traveling through fields. Body mass was the only predictor of gap crossing; lighter squirrels were more likely than were heavier squirrels to cross crop fields. Squirrels did not appear to base gap-crossing decisions on detour efficiency (distance to home crossing gap divided by distance of detour). Additionally, likelihood of homing within 24 hrs of release decreased with increasing crossing distance. The importance of body mass in gap crossing decisions by both *P. franklinii* and forest-dwelling red squirrels (*Tamiasciurus hudsonicus*) suggests a general pattern in which sciurid movements through heterogeneous landscapes are partly explained by trade-offs between predation risk and energetic constraints.

Key words: body mass, connectivity, detour efficiency, giving-up density, homing, movement trade-offs, translocation, predation risk, travel speed

INTRODUCTION

Dispersal of organisms among patches of habitat is essential for maintaining demographic and genetic connectivity (Hanski and Gaggiotti 2004). In fragmented landscapes, dispersal requires organisms to traverse inhospitable matrix habitats, increasing energetic costs and risk of mortality (Sakai and Noon 1997; Smith and Batzli 2006). The ability to cross these habitat gaps is influenced by the perceptive, cognitive, and movement capabilities of a species, as well as landscape composition and configuration (Bélisle and Desrochers 2002; Goodwin and Fahrig 2002; Rail et al. 1997; van der Ree 2003; Zollner 2000). Empirical data on how individuals move through heterogeneous habitats are needed to guide management actions, such as corridor establishment, to improve connectivity for species (Crooks and Sanjayan 2006; Hilty et al. 2006; Zollner and Lima 2005).

Functional connectivity for a species has two components: the likelihood of an individual entering matrix habitat and the likelihood of successfully reaching new suitable habitat once in the matrix (Ewers and Didham 2006; Kuefler et al. 2010; Rizkalla and Swihart 2007).

Individuals faced with a decision of entering matrix habitat or detouring around it balance trade-offs between predation risk, energetic cost of travel, and ability to perceive distant, suitable habitat (Zollner and Lima 2005). Species-specific characteristics such as perceptual capabilities or antipredatory behaviors (Zollner 2000; Zollner and Lima 2005) may affect how a species balances trade-offs. Nevertheless, general relationships determining movement through heterogeneous landscapes are likely (Wiens et al. 1993). Some behavioral trade-offs are well

documented, such as the inverse relationship between predation risk and foraging profitability for small animals in open versus dense vegetation (Brown 1988; Kotler and Blaustein 1995; Lima and Dill 1990). Few studies, however, examine how these relationships influence long-distance movement through heterogeneous landscapes (Bélisle and Desrochers 2002; Lima and Zollner 2006). Zollner and Lima (2005) used simulation models to investigate trade-offs between vigilance, foraging, and speed of movement faced by individuals dispersing through patchy landscapes. Dispersal success was greatest for individuals with high energy reserves that slowed to be vigilant, but because individuals with low reserves could not afford to slow, their success was greatest when they moved as quickly as possible (Zollner and Lima 2005). In addition, if options for reducing risk of predation while traveling through high-risk habitat are limited (e.g., no cover is available), individuals should minimize risk by traveling at faster speeds than in less risky habitats (Zollner and Lima 2005). Empirical data support these predictions, but are scant (Bakker and Van Vuren 2004; Bond et al. 2001; Kuefler et al. 2010; Rizkalla and Swihart 2007; Schtickzelle et al. 2007; Vásquez et al. 2002).

Researchers have studied movement decisions by tracking individuals induced to cross gaps in fragmented habitat by either displacement (Bakker and Van Vuren 2004; Bélisle and Desrochers 2002; Boscolo et al. 2008; Bowman and Fahrig 2002; Gillies and St. Clair 2008) or playback calls (Creegan and Osborne 2005; Robertson and Radford 2009). Gap-crossing experiments are useful for examining movement trade-offs because researchers can replicate and standardize motivation for movement, distance to a destination, and landscape composition and configuration encountered between release site and destination (Bélisle et al. 2001; Bright 1998; Desrochers and Hannon 1997; Pither and Taylor 1998). Studies of gap crossing have shown that individuals displaced across gaps in forest can balance long detour distances around gaps with

the risk of a shortcut through a gap by crossing gaps when detour efficiency (crossing distance divided by detour distance) is low (Bakker and Van Vuren 2004; Bélisle et al. 2001; Bélisle and Desrochers 2002; Desrochers and Hannon 1997; St. Clair et al. 1998). Bakker and Van Vuren (2004) also found adult *Tamiasciurus hudsonicus* (red squirrels) with low body mass were more likely to cross gaps in forest for any given detour efficiency than were heavier squirrels, possibly because low energy reserves forced riskier behavior, as predicted by Zollner and Lima (2005). Determining if this trade-off between body condition and risky movement is a generality requires investigations of additional species.

Studies of gap-crossing behavior have focused on forest-dwelling animals (e.g., Bakker and Van Vuren 2004; Bélisle and Desrochers 2002; Boscolo et al. 2008; Creegan and Osborne 2005; Gillies and St. Clair 2008). In the Midwestern U.S., grassland habitat is severely fragmented by row-crop agriculture and urbanization and has suffered extensive loss of area (Samson and Knopf 1994). Remnant grasslands occur as prairie reserves and as linear stretches along roadsides and railroad rights-of-way within a mosaic of crop fields (Duggan et al. 2011). Connectivity between patches of grassland habitat is likely low for many species including those of conservation concern (Samson and Knopf 1994). Empirical data on gap-crossing by grassland species are needed to manage for connectivity and to test the generality of movement trade-offs in heterogeneous landscapes.

I tested if gap-crossing decisions and homing success by *Poliocitellus franklinii* (Franklin's ground squirrel) translocated across crop fields were the result of trade-offs between travel cost and predation risk. *Poliocitellus franklinii* (formerly *Spermophilus franklinii*; Helgen et al. 2009) inhabits areas with tall, dense grasses and occurs at low densities in the Midwest. The species is listed as endangered in Indiana, threatened in Illinois, and a species of special

concern in Iowa, Missouri, and Wisconsin. Grassland patches occupied by *P. franklinii* are typically inhabited by ≤ 20 adult squirrels (Martin et al. 2003; Martin and Heske 2004) and are presumed subpopulations linked by dispersal. Indeed, a study of occupancy dynamics for *P. franklinii* demonstrated site occupancy was related positively to connectivity, and local extinction was related negatively to connectivity (Duggan et al. 2011). As with other species of ground squirrels, male-biased dispersal is undertaken by juveniles in late summer and early autumn during their first year of life. Crops are typically at full height during dispersal, and both movements of radiomarked juveniles (Martin and Heske 2005) and predictions of site occupancy using least-cost modeling (Duggan et al. 2011) suggest movement occurs through agricultural habitat. However, crop fields are unplanted in spring when adults emerge from hibernation, establish home ranges, and search for mates. Thus, in spring and early summer, individuals facing a decision to either enter a fallow crop field or detour around it likely balance trade-offs similar to forest animals encountering a clearcut. I therefore assessed potential predictors for the likelihood of squirrels crossing crop fields and successfully homing in spring and early summer. Predictors included traits inherent to individuals (sex, body mass) and aspects of landscape structure (e.g., crossing distance, detour efficiency, crop height).

I expected *P. franklinii* would perceive a higher risk of predation in open crop fields than in grass habitat and differences in perceived risk would create a trade-off for translocated squirrels between traveling through high-risk crop fields or taking an energetically more costly detour around crop fields to return home. I tested two hypotheses regarding gap-crossing decisions made by squirrels faced with this trade-off. First, I tested the hypothesis that squirrels base gap-crossing decisions on lengths of alternate movement routes. If squirrels balance predation risk versus travel cost in gap-crossing decisions, likelihood of crossing a high-risk crop

field should increase when detour efficiency is low. Second, I tested the hypothesis that squirrels base gap-crossing decisions on individual energetic constraints. If energetic cost is the primary factor in decisions to cross risky habitat, likelihood of crossing a crop field should increase if body mass of an individual is low. I gathered supporting evidence for the role of perceived risk of predation in gap-crossing decisions by testing if both perceived risk and travel speed were greater in crop fields than in grass habitat. Last, to determine if *P. franklinii* experienced a threshold distance at which individuals were unable to navigate home, I examined the relationship between crossing distance and homing. A threshold would indicate a distance at which functional connectivity for *P. franklinii*, and likelihood of metapopulation persistence, would decrease.

METHODS

FILED CROSSING AND HOMING

From April-July 2010, I livetrapped *P. franklinii* at two locations: restored prairie habitat in the Barnhart Prairie Nature Preserve in Champaign Co., IL and remnant prairie along railroad rights-of-way in Vermilion Co., IL. Both locations were within agricultural landscapes and surrounded by a mosaic of corn and soybean fields, farm lots, and low-traffic roads. Unmowed cool-season grasses, dominated by smooth brome (*Bromus inermis*), bordered crop fields and roads. I set Tomahawk live traps (model 202, Tomahawk Live Trap, Tomahawk, Wisconsin) baited with peanut butter and sunflower seeds in prairie habitat and unmowed grasses within 100 m of corn and soybean crop fields. Trap number and spacing varied according to shape and extent of grassland habitat, and locations of ground squirrel burrows. I set traps before 0800 h, checked traps at 2-h intervals, and closed traps for the day by 1300 h. I covered traps with

vegetation to protect captured squirrels from sun and shut traps during rain. I recorded age (juvenile or adult), sex, reproductive condition, and mass of each captured individual. I radiocollared squirrels weighing > 250 g using transmitters with activity switches (model M 1540, Advanced Telemetry Systems Inc., Isanti, Minnesota) mounted on plastic cable ties. Collars each weighed 4.5 g and never exceeded 2% of body mass. Procedures followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the University of Illinois Institutional Animal Care and Use Committee.

To test if *P. franklinii* makes gap-crossing decisions based on trade-offs between travel cost and predation risk, I translocated radiomarked, adult squirrels off their home ranges, across crop fields, to unmowed grass habitat 87 to 1,527 m (mean = 470, $SE = 51$ m) away from centers of home ranges (Figure 3.1). During the study, I depended on capture locations of squirrels rather than home ranges to estimate translocation distances. Recording of telemetry locations for use in home range estimation at that time was constrained by trapping and translocation activities, driving between study sites in two counties, and the need to conduct experimental translocations while crops were still short. Following completion of translocations, I estimated home ranges with a 100% minimum convex polygons (MCP) model using Hawth's Analysis Tool for ArcGIS (Beyer 2004), based on an average of 16 telemetry locations (range = 5-25) obtained from April to August 2010 by signal homing using a receiver and handheld 3-element yagi antenna. This number of locations is smaller than typically used to estimate home range size (Seaman et al. 1999; Wauters et al. 2007), but I only used these data to identify areas to which we expected squirrels to home. I calculated home range centers as geometric centers of MCP polygons.

I translocated 17 individuals (8 males, 9 females) during 33 trials, releasing each squirrel between 1100 and 1530 h. I translocated 4 squirrels once, 10 squirrels twice, and 3 squirrels 3 times (Appendix B). Squirrels translocated more than once typically were taken to different release points on non-consecutive days (1 squirrel was translocated on 2 consecutive days). Female squirrels were not translocated if obviously pregnant (palpable embryos) or lactating. I conducted 26 translocations across soybean fields and 7 translocations were across corn fields. Although travel speeds of forest rodents can differ between soybean and corn fields (Rizkalla and Swihart 2007), I conducted all translocations when crop heights were low (≤ 40 cm) and vegetative cover was sparse, and assumed movements of *P. franklinii* would vary little with type of crop at these heights. Researchers transported each squirrel in a Tomahawk live trap while walking across a crop field in a straight line from capture to release locations. During transportation, the trap containing the squirrel was held above the researcher's head to provide visual information about location and potential routes home. To decrease the probability that squirrels were provided with scent information about potential routes home, I did not repeat use of release sites until after rain. At the release site, I attached a tracking spool (Bakker and Van Vuren 2004) between the shoulder blades of the squirrel using cyanoacrylate glue and placed the squirrel in a transparent plastic bin (28 x 34 x 28 cm). The bin was placed with its lid on the ground and its base attached with rope to a frame with a pulley system made of polyvinyl chloride (PVC) tubing. To release the squirrel, a researcher standing 10 m from the release location in the direction opposite the squirrel's capture location pulled the rope through the pulley system, raising the bin 0.5 m above the ground while leaving the lid and squirrel on the ground. Squirrels were able to move in any direction upon release and seemed unaffected by the presence of the researcher, in some cases initially moving directly towards the researcher.

I determined homing routes by tracking spool traces and with telemetry by 2-3 researchers simultaneously recording their locations with GPS and azimuths to squirrels at 3-min intervals. Telemetry locations were estimated with bi- and triangulation using LOAS 4.0 (Ecological Software Solutions LLC 2010). When 3 bearings were available, I used the Maximum Likelihood Estimator (MLE) and calculated error ellipses using the corrected F distribution and a 95% confidence interval, as well as angular error between bearings and estimated locations. When only 2 bearings were available, or I was unable to estimate a location using MLE, I used the best bi-angulation estimator and calculated angular error. I rejected triangulations with values of error in the top decile of the error distribution (error ellipse areas ≥ 10 ha and angular error averaged for 2-3 bearings $\geq 50^\circ$). The remaining triangulations had an average error ellipse area of 1.2 ha, and the average angular error was 15° . These errors were similar to average error ellipse area (0.9 ha) and average angular error (17°) for triangulated locations of eight radiotransmitters hidden in crop fields by an independent researcher. Average distance between hidden transmitters and triangulated locations was 13 m ($SE = 3$), excluding one outlier of 294 m. Because 1 researcher always conducted telemetry from the well-defined edge between grass habitat and crop field, I was confident of our ability to identify the habitat within which an individual was moving.

Potential predictors of field crossing and homing (defined as returning to a home range within 24 hrs of translocation release) included Julian date, location (Champaign versus Vermilion County), sex, body mass on date of translocation, crossing distance, and detour efficiency (crossing distance/detour distance; range = 0.36-1.0). I used ArcGIS 9.2 to measure crossing and detour distances (shortest distance from release point to center of home range avoiding crop field). Additionally, I estimated mean crop height (categorized into 10 cm

increments) during each translocation and included it as a predictor in models, as increases in crop height could decrease perceived risk of predation for crop fields. Prior to model construction, I examined a Pearson correlation coefficient (r) matrix for potential collinearity between predictors, and predictors with $r > 0.6$ were not included together in models. I conducted a repeated-measures analysis (GLIMMIX procedure, SAS 9.2, SAS Institute Inc., 2009) to test which predictors significantly influenced field crossing and homing. I used a binomial distribution and logit link function for both responses. Trial (1st, 2nd, and 3rd translocation of squirrel) was the repeated measure, and I modeled the covariance structure using variance components. I estimated degrees of freedom for F -tests using the Kenward-Roger method. Because of our moderate sample size, I considered predictors significant at $P < 0.1$ for these analyses and all described hereafter.

PERCEIVED PREDATION RISK

I used a measure of giving-up density (GUD; Brown 1988) to test if perceived risk of predation by *P. franklinii* was greater in crop fields, where cover from predators was minimal, than in tall grasses (prairie and unmowed grass >40 cm high). A GUD is the amount of resources remaining in a depletable resource patch after a set period of time that includes foraging (i.e., density of resources remaining when a forager “gives up”). When multiple patches of similar size and food resources are available to a forager, GUD increases with perceived risk of predation (Brown 1988; Brown et al. 1988; Thorson et al. 1998).

To measure GUD, I used experimental food patches consisting of plastic nursery trays (55 x 28 x 6 cm) holding 50 shelled peanuts mixed into 4 l of commercial sand. I used peanuts to allow foraging by *P. franklinii*, but discourage foraging by birds. Each day after sunrise, I

provisioned trays with 50 peanuts and left trays open to foraging during the day. Between 1700 and 1800, I sieved and counted peanuts remaining in each tray to determine daily GUD for each patch. I covered trays with lids overnight to prevent accumulation of moisture in the sand. I created 5 stations at our study site in Champaign County, each 100-800 m apart. At each station, I placed one food patch in tall grasses 3 m from a grass-crop field edge and a second food patch in the adjacent crop field 3 m from the same edge. At these distances, individuals may have occasionally encountered multiple stations, but could easily encounter both food patches at a station (Morgan et al. 1997).). I did not observe diurnal mammalian foragers other than *P. franklinii* near stations and I observed no evidence of birds using our stations; however, on one occasion I captured a *Sciurus carolinensis* (eastern grey squirrel) near a station. I ran GUD stations in 5-6 day sessions; days were consecutive when rain did not occur. Three of 5 stations were run for a session in early June 2010, and all 5 stations were run for a session in early July 2010.

I used the GLIMMIX procedure to test if GUD differed between tall grass and crop field habitats and considered day a repeated measure. I also tested if GUD differed among stations and if there was an interactive effect between habitat and stations. I used a normal distribution and an identity link. I modeled the covariance structure using variance components and estimated degrees of freedom using the Kenward-Roger method.

TRAVEL SPEED

To test if travel speed was greater in crop fields than in tall grass habitat, I used Hawth's Analysis Tool (Beyer 2004) in ArcGIS 9.2 to create movement paths from triangulated locations, excluding triangulations associated with the top decile of error values, and determined the habitat

in which each triangulated location occurred. When ≥ 2 consecutive locations occurred in one type of habitat, I estimated speed of travel through the habitat by dividing net distance traveled between the first and last location by the time recorded between triangulations. I excluded the first 3-min time interval and any extended latency period (i.e., < 20 m moved between triangulated locations; Bakker and Van Vuren 2004) following release. By using net distance to calculate travel speed, I included pauses in travel used for antipredatory behavior, orientation, or physiological recovery, as well as changes in direction of movement associated with a search strategy. When a squirrel had multiple bouts of travel within a habitat type during a translocation, I averaged estimates across bouts.

I used the GLIMMIX procedure to test if travel speeds differed between tall grass and crop field habitats, as well as with sex, body mass or travel route (cross versus detour). After censoring latency periods and locations with high error, I was able to calculate travel speeds for 14 of 33 translocations. Data included travel speed for repeated translocations on only four individuals. Rather than use repeated-measures, I included travel speeds for the earliest translocation of each individual and included trial number as a predictor, as the earliest translocation of each individual was not always the first trial, due to censoring. The distribution of travel speeds was positively skewed, so I used a Gamma distribution with a log link. I modeled the covariance structure using variance components and estimated degrees of freedom using the Kenward-Roger method.

RESULTS

FIELD CROSSING AND HOMING

Squirrels crossed a crop field in 8 (24%) of 33 translocations (22 in Champaign County and 11 in Vermilion County). One squirrel began detouring around a crop field, moving 130 m through roadside grasses before traveling 240 m across the field; because that individual traveled nearly twice as far while crossing than detouring, I classified the trial as a field crossing.

Squirrels homed in 28 (85%) of 33 translocations. Seven (88%) of 8 trials in which squirrels crossed a crop field resulted in homing, and 21 (84%) of 25 trials in which squirrels detoured resulted in homing. We livetrapped squirrels that did not home and returned them to their original capture sites.

Julian date was strongly correlated with both body mass of squirrels ($r = 0.62$) and crop height ($r = 0.92$). Therefore, I excluded Julian date as a predictor variable in my models examining field crossing and homing, but included location, sex, body mass, crossing distance, detour efficiency, and crop height. Body mass was the only predictor of field crossing ($F_{1, 27} = 3.45$, $P = 0.074$; Figure 3.2); squirrels that crossed fields were lighter (mean = 402 g, $SE = 33$ g) than were squirrels that detoured (mean = 454 g, $SE = 10$ g). Crossing distance was the only predictor of homing ($F_{1, 27} = 3.88$, $P = 0.059$; Figure 3.3); squirrels that homed were translocated shorter distances (mean = 433 g, $SE = 56$ m) than were squirrels that did not reach home (676 ± 89 m).

PERCEIVED PREDATION RISK

GUD was greater in crop fields (31.8 ± 2.9 peanuts/patch) than tall grasses (12.6 ± 2.3 peanuts/patch; $F_{1, 82} = 27.02$, $P < 0.001$; Figure 3.4). GUD also varied among stations ($F_{4, 82} =$

8.41, $P < 0.001$) but there was no interaction between habitat and station ($F_{4, 82} = 0.21$, $P > 0.932$). Two patches in crop fields might not have been visited during a session (all peanuts remained in a patch ≥ 5 days). To separate results due to perceived predation risk from those due to non-visitation, I analyzed a reduced data set with patches without visitation removed. GUD again was greater in crop fields (26.6 ± 3.4 peanuts/patch) than in tall grasses (11.8 ± 2.6 peanuts/patch; $F_{1,70} = 16.69$, $P < 0.001$) and varied among stations ($F_{4,70} = 9.71$, $P < 0.001$).

TRAVEL SPEED

Travel speeds in crop fields averaged 8.5 m/min ($SE = 2.8$ m/min), whereas travel speeds in grass averaged 5.3 m/min ($SE = 1.6$ m/min), but the difference was not significant ($F_{1,23} = 1.34$, $P > 0.258$). Travel speed also did not vary predictably with body mass ($F_{1,23} = 1.31$, $P > 0.265$) or travel route ($F_{1,23} = 0.45$, $P > 0.507$). Travel speed differed between sexes ($F_{1,23} = 4.88$, $P < 0.037$), however, with males (mean = 9.3 m/min, $SE = 2.4$ m/min) moving faster than females (n = 7 males, 7 females, mean = 4.4 m/min, $SE = 1.6$).

DISCUSSION

The grassland habitats occupied by *P. franklinii* in the Midwestern U.S. exist as highly fragmented patches in an agriculturally dominated landscape. In spring and early summer, crop fields harbor little vegetative cover and act as inhospitable matrix. Responses by adult *P. franklinii* to this open habitat are analogous to responses by forest-dwelling species to clearcuts; our GUD data indicated *P. franklinii* perceived a higher risk of predation in crop fields than in grass, and translocations demonstrated most squirrels chose detours around crop fields when homing. Squirrels did not appear to base gap-crossing decisions on detour efficiency, but rather

on trade-offs between predation risk and energetic constraints. Despite a perception of increased predation risk for crop fields, travel speed was not strongly adjusted by squirrels to compensate for this risk when traveling through fields.

Lack of support for the hypothesis that *P. franklinii* would base gap-crossing decisions on detour efficiency contrasts with studies on gap crossing by forest-dwelling birds and mammals (Bakker and Van Vuren 2004; Bélisle et al. 2001; Bélisle and Desrochers 2002; Desrochers and Hannon 1997; St. Clair et al. 1998). Only animals with a large perceptual range are likely to have the capacity to compare movement routes before selecting one (Bakker and Van Vuren 2004; Lima and Zollner 1996). Although the relatively large body size of *P. franklinii* (340-800 g; Hofmann 2008) suggests a large perceptual range (Kiltie 2000; Mech and Zollner 2002), burrowing habits and preference for dense vegetation may render *P. franklinii* unable, or unaccustomed, to using visual information as provided in this study to compare movement routes. However, observations of spool traces suggested squirrels oriented along either a crossing or detour route within the first 100 m of travel. Further, squirrels reached their home ranges within 24 h in 85% of translocations. Thus, squirrels likely were selecting movement routes to return home, even if not basing route selection on detour efficiency.

The importance of body mass in gap crossing decisions by both *P. franklinii* and *T. hudsonicus* (Bakker and Van Vuren 2004) suggests a general pattern in which sciurid movements through heterogeneous landscapes are partly explained by trade-offs between predation risk and energetic constraints (Zollner and Lima 2005). *P. franklinii* generally risked shortcuts across crop fields when potentially limited by energy reserves (i.e., low body mass). I did not evaluate actual physical condition such as ratios of body mass to length, which would have required sedating squirrels for handling. The lightest individuals in our study could have

been in the poorest condition, or may have been the youngest squirrels. Effects of condition and age on gap-crossing decisions by *P. franklinii* deserve closer examination. In addition, overwinter mass loss can be 44% of summer body mass for *P. franklinii* (Murie 1973), thus energetic constraints might especially affect movement decisions immediately following emergence (when I began translocations), before squirrels replenish energetic reserves consumed during hibernation. Future research should investigate the generality of trade-offs between body condition and risky movement, as well as how such trade-offs influence movement decisions by species that undergo periods of severe energy constraints.

Similar to Bakker and Van Vuren (2004), I detected small differences in travel speed by squirrels in high-risk versus low-risk habitats. Bakker and Van Vuren (2004) found *T. hudsonicus* tended to move at slower travel speeds while crossing clearcuts than detouring through forest, possibly because dense shrubs and herbs in clearcuts impeded movement (Schooley et al. 1996) or obstructed detection of predators and stimulated vigilance behavior (Sharpe and Van Horne 1998). In my study, however, cover in crop fields was minimal to nonexistent. Thus, I expected *P. franklinii* to compensate for risk in crop fields by increasing travel speed, similar to other organisms traveling through open habitats that are risky or lack resources (Bond et al. 2001; Kuefler et al. 2010; Rizkalla and Swihart 2007; Schtickzelle et al. 2007; Vásquez et al. 2002). However, I found only a minimal increase in travel speed by *P. franklinii* in crop fields relative to grass habitat. Travel speeds of males were faster than speeds of females in both habitats. Post hoc analyses indicated no interactions between sex and habitat type or sex and movement route explaining travel speed, suggesting difference in travel speed between sexes was not due to differences in perceived predation risk. Furthermore, there was no interaction between sex and body mass, indicating sexual dimorphism in body mass did not

explain difference in travel speed. Males typically have larger home ranges and move longer distances than females, especially in spring when males are seeking females with which to mate (Martin and Heske 2005; J. M. Duggan, Pers. Obs.). Although homing success did not vary between sexes, perhaps familiarity with long distance movements promoted faster travel speed in males than females.

For sciurids, homing success decreases with increased translocation distance (Bovet 1984; Sawyer and Rose 1985; Smith et al. 2011; Van Vuren et al. 1997). Not surprisingly, likelihood of *P. franklinii* homing within 24 h of translocation decreased with increasing crossing distance. However, this result appears driven by the high success rate after short translocations rather than failure of squirrels translocated longer distances to home (Figure 3.3). Interestingly, the individual translocated the longest crossing distance in our study (1,527 m) homed within 24 h in Vermilion County. Interception effects (Gutzwiller and Anderson 1992) may have played a role in homing success in Vermilion County, as home ranges along the linear railroad habitat in Vermilion County were long and thin, and likely to be intercepted by a traveling animal. Interception of squirrels by grasslands, whether inhabited or not, suggest configuration of habitat patches might be an important predictor of dispersal success in this highly linearized landscape. Indeed, Schippers et al. (2009) used simulation models to demonstrate linear elements in an agricultural landscape could intercept and guide dispersing woodland birds between habitat patches, increasing connectivity and metapopulation persistence.

For animals living in agricultural landscapes, connectivity can vary seasonally with changes in crop height (Goheen et al. 2003; Rizkalla and Swihart 2007). Whereas long-distance movements of *P. franklinii* are typically thought to occur via juvenile dispersal in autumn when crop heights and connectivity are at a maximum, this may not always be true. In 2010, I

radiotracked 21 juvenile male *P. franklinii* in Champaign County. Whereas Martin and Heske (2004) found juvenile male *P. franklinii* traveled 614 - 3,632 m before immergence, I tracked only one movement by a juvenile >700 m before immergence, suggesting an unknown factor repressed juvenile dispersal during autumn 2010. Long-distance movements by over-wintered adults in the spring might play a role in maintaining demographic and genetic stability of *P. franklinii* populations. The importance of long-distance breeding forays in reducing inbreeding has been documented for philopatric populations of banner-tailed kangaroo rats (*Dipodomys spectabilis*; Winters and Waser 2003).

Our study demonstrates how loss and fragmentation of grassland habitat have shaped variation in predation risk and travel costs across agriculturally dominated landscapes, and thus the trade-offs on which *P. franklinii* bases movement decisions. Further, combined with previous research on gap-crossing by sciurids (Bakker and Van Vuren 2004), our results suggest the trade-off between predation risk and energetic constraint may act as a general relationship describing movement of sciurids through heterogeneous landscapes. Identifying general relationships that govern movements of a species through landscapes is needed to understand functional connectivity and to determine appropriate strategies for conservation and management (Crooks and Sanjayan 2006; Hilty et al. 2006). High homing success by translocated squirrels suggests *P. franklinii* can be adept at moving across an agricultural landscape, but the low frequency of field crossing cautions that fallow fields in early spring may be areas of high predation risk that inhibit movements and gene flow during the mating season. However, *P. franklinii* will inhabit linear habitats and use them as routes of travel, and if travel costs are not too high, simple actions such as reducing mowing of grasses along linear roads and railways could increase use of linear elements and increase connectivity for *P. franklinii*.

ACKNOWLEDGMENTS

I would like to thank the Layden and Smith families for allowing us to conduct translocations through their crop fields. I am also grateful to the Barnhart family for allowing us access to private property adjacent to the Barnhart Prairie Nature Preserve. I thank L. Buckingham, S. Fredebaugh-Siller, L. Pritchard, A. Keever, and J. Rydzewski for field assistance. This project was funded by the Illinois Department of Natural Resources through the Federal Aid in Wildlife Restoration Program (Project W-152-R), University of Illinois, and Prairie Biotic Research, Inc. Small Grants Program.

REFERENCES

- BAKKER, V. J., AND D. H. VAN VUREN. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology* 18:689–697.
- BÉLISLE, M., A. DESROCHERS, AND M.-J. FORTIN. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82:1893-1904.
- BÉLISLE, M., AND A. DESROCHERS. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* 17:219-231.
- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatialecology.com/htools>.
- BOND, B. T., B. D. LEOPOLD, L. W. BURGER, JR., K. D. GODWIN. 2001. Movements and home range dynamics of cottontail rabbits in Mississippi. *Journal of Wildlife Management*. 65:1004-1013.
- BOSCOLO, D., C. CANADIA-GALLARDO, M. AWADE, AND J. P. METZGER. 2008. Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (*Xiphorhynchus fuscus*) in the Atlantic Forest, Brazil. *Biotropica* 40:273-276.
- BOVET, J. 1984. Strategies of homing behavior in the red squirrel, *Tamiasciurus hudsonicus*. *Behavior, Ecology, and Sociobiology* 16:81-88.
- BOWMAN, J., AND L. FAHRIG. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology* 80:1556-1561.
- BRIGHT, P. 1998. Behavior of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour* 56:1485-1490.

- BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37-47.
- BROWN, J. S., B. P. KOTLER, R. J. SMITH, AND W. O. WIRTZ II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76:408-415.
- CREEGAN, H. P., AND P. E. OSBORNE. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. *Journal of Applied Ecology* 42:678-687.
- CROOKS, K. R. AND M. SANJAYAN. 2006. Connectivity conservation: maintaining connections for nature. Pp. 1-20 in *Connectivity conservation* (K. R. Crooks and M. Sanjayan, eds.). Cambridge University Press, New York.
- DESROCHERS, A., AND S. J. HANNON. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11:1204-1210.
- DUGGAN, J. M., R. L. SCHOOLEY, AND E. J. HESKE. 2011. Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? *Landscape Ecology* 26:1477-1490.
- EWERS, R. M., AND R. K. DIDHAM. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117-142.
- GILLIES, C. S., AND C. C. ST. CLAIR. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences of the United States of America* 105:19774-19779.
- GOHEEN, J. R., R. K. SWIHART, T. M. GEHRING, AND M. S. MILLER. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos* 102:95-103.

- GOODWIN, B. J., AND L. FAHRIG. 2002. How does landscape structure influence landscape connectivity? *Oikos* 99:552-570.
- GUTZWILLER, K. J., AND S. H. ANDERSON. 1992. Interception of moving organisms: influences of patch shape, size, and orientation on community structure. *Landscape Ecology* 6:293-303.
- HANSKI, I., AND O. E. GAGGIOTTI. 2004. Ecology, evolution, and genetics of metapopulations. Academic Press, San Diego, California.
- HELGES, K. M., F. R. COLE, L. E. HELGES, AND D. E. WILSON. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. *Journal of Mammalogy* 90:270-305.
- HILTY, J. A., W. Z. LIDICKER JR., AND A. M. MERENLENDER. 2006. Corridor ecology. Island Press, Washington, DC.
- HOFMANN, J. E. 2008. Field manual of Illinois mammals. Illinois Natural History Survey, Champaign.
- KILTIE, R. A. 2000. Scaling of visual acuity with body size in mammals and birds. *Functional Ecology* 14:226-234.
- KOTLER, B. P. AND L. BLAUSTEIN. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? *Oikos* 74:251-258.
- KUEFLER, D., B. HUDGENS, N. M. HADDAD, W. F. MORRIS, AND N. THURGATE. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. *Biological Reviews* 91:944-950.
- LIMA, S. L. AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.

- LIMA, S. L., AND P. A. ZOLLNER. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131-135.
- MARTIN, J. M., AND E. J. HESKE. 2004. Cover and soil drainage influence burrow location of Franklin's ground squirrel (*Spermophilus franklinii*) in Champaign County, Illinois. *Transactions of the Illinois State Academy of Science* 97:227-233.
- MARTIN, J. M., AND E. J. HESKE. 2005. Juvenile dispersal of Franklin's ground squirrel (*Spermophilus franklinii*) from a prairie "island". *American Midland Naturalist* 153:444-449.
- MARTIN, J. M., E. J. HESKE, AND J. E. HOFMANN. 2003. Franklin's ground squirrel in Illinois: a declining prairie mammal? *American Midland Naturalist* 150:130-138.
- MECH, S. G., AND P. A. ZOLLNER. 2002. Using body size to predict perceptual range. *Oikos* 98:47-52.
- MORGAN, R. A., BROWN, J. S., AND J. M. THORSON. 1997. The effect of spatial scale on the functional response of fox squirrels. *Ecology* 78:1087-1097.
- MURIE, J. O. 1973. Population characteristics and phenology of a Franklin ground squirrel (*Spermophilus franklinii*) colony in Alberta, Canada. *American Midland Naturalist* 90:334-340.
- PITHER, J., AND P. D. TAYLOR. 1998. An experimental assessment of landscape connectivity. *Oikos* 83:166-174.
- RAIL, J.-F., M. DARVEAU, A. DESROCHERS, AND J. HUOT. 1997. Territorial responses of boreal forest birds to habitat gaps. *Condor* 99:976-980.
- RIZKALLA, C. E., AND R. K. SWIHART. 2007. Explaining movement decisions of forest rodents in fragmented landscapes. *Biological Conservation* 140:339-348.

- ROBERTSON, O. J., AND J. Q. RADFORD. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. *Austral Ecology* 34:435-446.
- SAKAI, H. F., AND B. R. NOON. 1997. Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *Journal of Wildlife Management* 61:343-350.
- SAMSON, F., AND F. KNOPF. 1994. Prairie conservation in North America. *BioScience* 44:418-421.
- SAWYER, S. L., AND R. K. ROSE. 1985. Homing in and ecology of the southern flying squirrel *Glaucomys volans* in Southeastern Virginia. *American Midland Naturalist* 113:238-244.
- SCHIPPERS, P., C. J. GRASHOF-BOKDAM, J. VERBOOM, J. M. BAVECO, R. JOCHEM, H. A. M. MEEUWSEN, M. H. C. VAN ADRICHEM. 2009. Sacrificing patches for linear elements enhances metapopulation performance of woodland birds in fragmented landscapes. *Landscape Ecology* 24:1123-1133.
- SCHOOLEY, R. L., P. B. SHARPE, AND B. VAN HORNE. 1996. Can shrub cover increase predation risk for a desert rodent? *Canadian Journal of Zoology* 74:157-163.
- SCHTICKZELLE, N., A. JOIRIS, H. VAN DYCK, AND M. BAGUETTE. 2007. Quantitative analysis of changes in movement behavior within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7:1471-1487.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND T. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- SHARPE, P. B., AND B. VAN HORNE. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). *Journal of Mammalogy* 79:906-918.

- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.
- SMITH, J. E., AND G. O. BATZLI. 2006. Dispersal and mortality of the prairie vole, *Microtus ochrogaster*, in fragmented landscapes: a field experiment. *Oikos* 112:209-217.
- SMITH, M. J., M. G. BETTS, G. J. FORBES, D. G. KEHLER, M. C. BOURGEOIS, AND S. P. FLEMMING. 2011. Independent effects of landscape connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecology* 26:709-721.
- ST. CLAIR, C. C., M. BÉLISLE, A. DESROCHERS, AND S. HANNON. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology* [online] 2:13.
- THORSON, J. M., R. A. MORGAN, J. S. BROWN, AND J. E. NORMAN. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behavioral Ecology* 9:151-157.
- TREMBLAY, M. A., AND C. C. ST. CLAIR. 2011. Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *Journal of Applied Ecology* 48:679-688.
- VAN DER REE, R., A. F. BENNETT, AND D. C. GILMORE. 2003. Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. *Biological Conservation* 115:241-249.
- VAN VUREN, D., A. J., KUENZI, I. LOREDO, AND M. L. MORRISON. 1997. Translocation as a nonlethal alternative for managing California ground squirrels. *Journal of Wildlife Management* 61:351-359.

- VÁSQUEZ, R. A., L. A. EBENSPERGER, AND F. BOZINOVIC. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology* 13:182-187.
- WAUTERS, L. A., D. G. PREATONI, A. MOLINARI, G. TOSI. 2007. Radio-tracking squirrels: performance of home range density and linkage estimators with small range and sample size. *Ecological Modelling* 222:333-344.
- WIENS, J. A., N. C. STENSETH, B. VAN HORNE, AND R. A. IMS. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369-380.
- WINTERS, J. B., AND P. M. WASER. 2003. Gene dispersal and outbreeding in a philopatric mammal. *Molecular Ecology* 12:2251-2259.
- ZOLLNER, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* 15:523-533.
- ZOLLNER, P. A., AND S. L. LIMA. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos* 108:219-230.

FIGURES

Figure 3.1 Image of crop field at which multiple translocations of *Poliocitellus franklinii* were conducted during April-June 2010 in Vermilion County, Illinois. Individuals were captured in remnant prairie along the railroad (RR) and translocated across a crop field to unmowed grass adjacent to a road. Open circle = centroid of home range for one translocated individual. Open square = example release point. Dotted black line represents route crossing crop field. Dashed black line represents route detouring through grass around crop field.

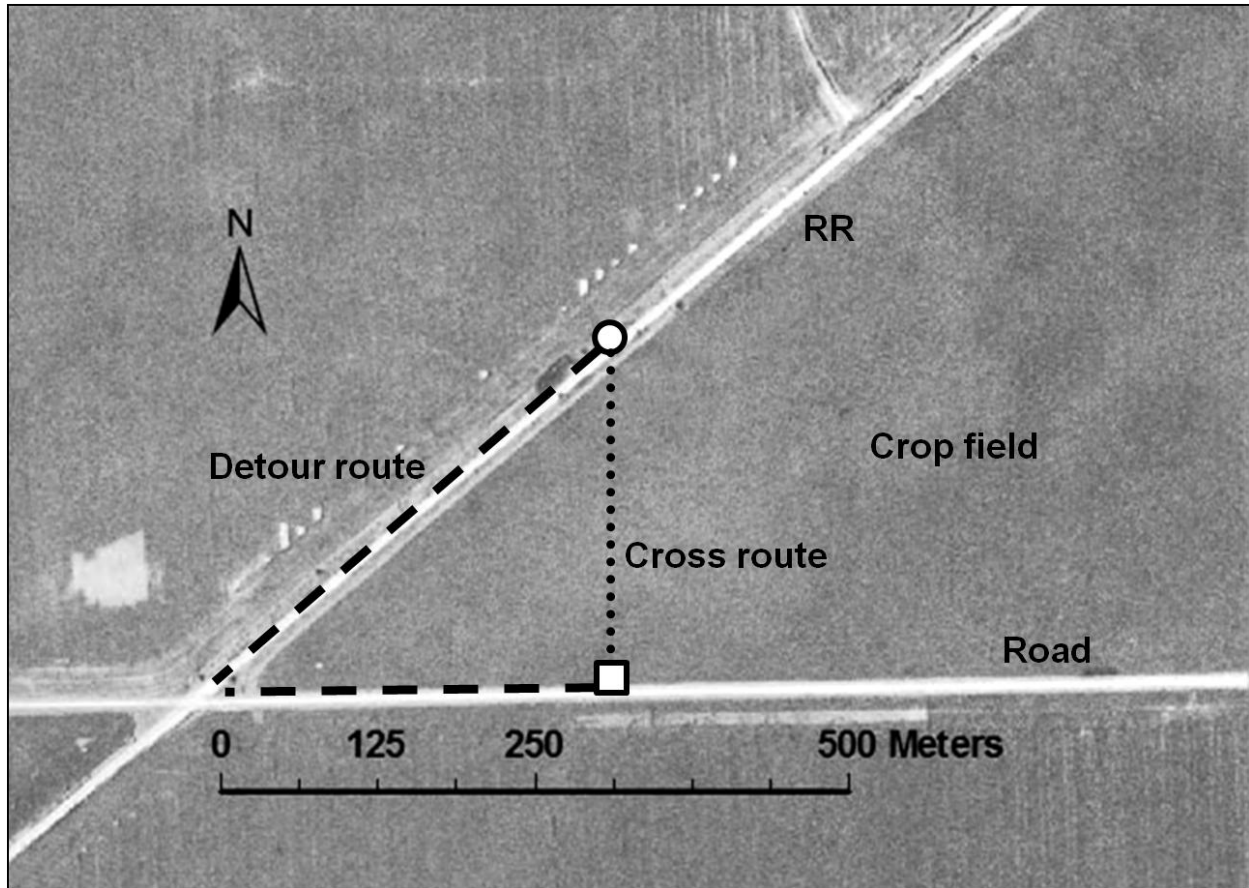


Figure 3.2 Probability of field crossing (open circles) as predicted by body mass of adult *Poliocitellus franklinii* (Franklin's ground squirrel) translocated from home ranges in east-central Illinois, 2010. Probabilities estimated with a logistic regression. Filled circles indicate trials in which individuals crossed (0.5) or detoured (0) around a crop field

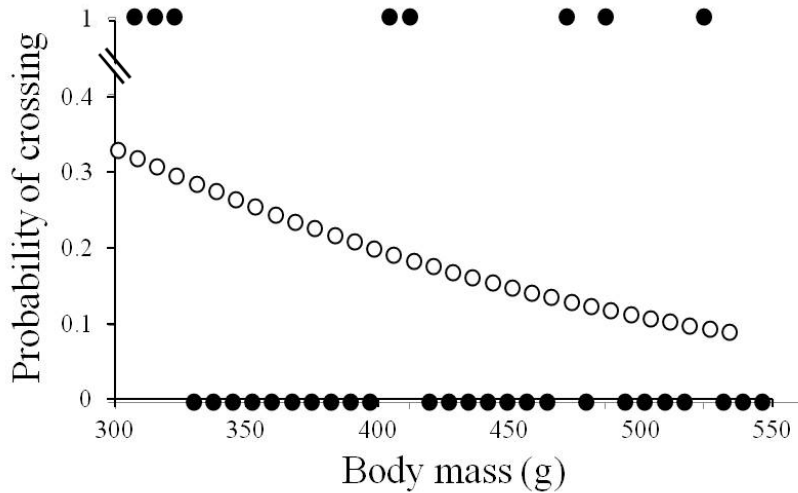


Figure 3.3 Probability of homing within 24 hrs (open circles) as predicted by crossing distance from release location to centroid of home range for translocated *Poliocitellus franklinii*. Translocations were conducted in east-central Illinois, 2010. Probabilities estimated with a logistic regression. Filled circles indicate trials in which individuals homed successfully (1) or failed (0)

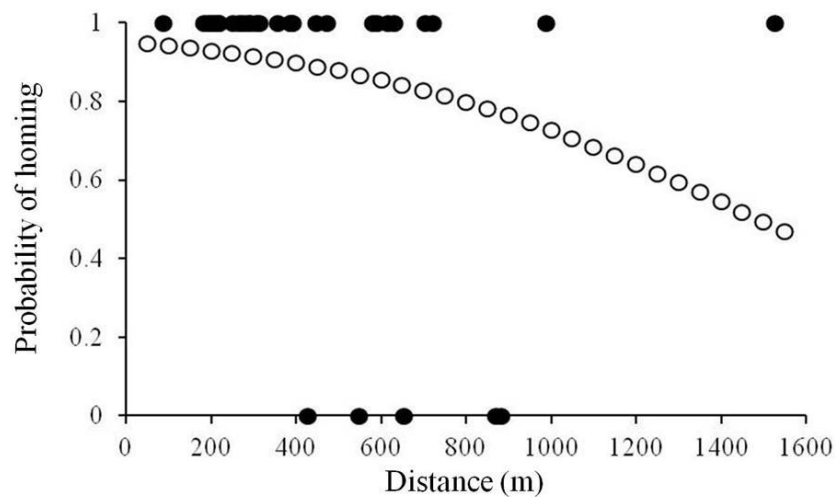
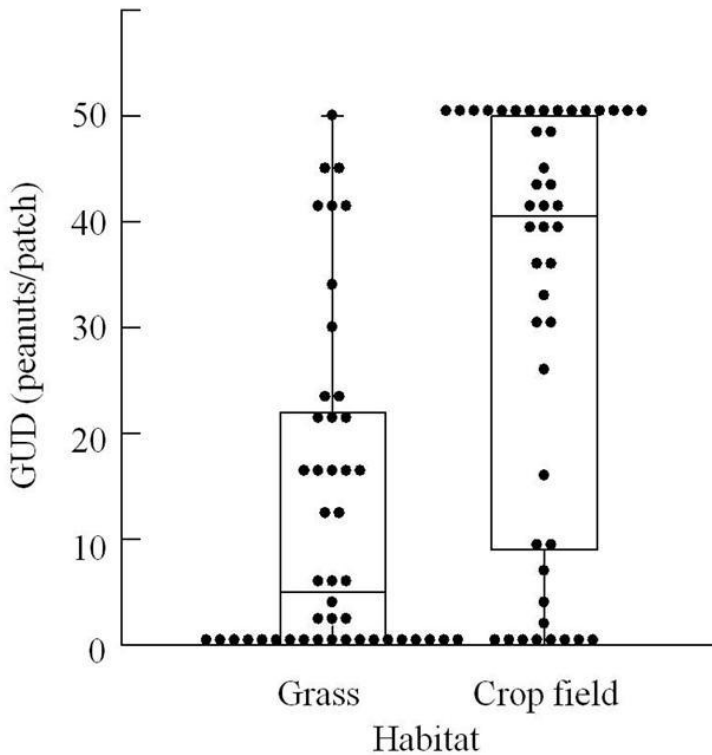


Figure 3.4 Box plots comparing GUD (giving-up density) for *Poliocitellus franklinii* (Franklin's ground squirrel) in resource patches set in grassland and crop field habitats in east-central Illinois, June-July 2010. Boxes represent 25th and 95th percentiles, horizontal lines within boxes indicate medians, and whiskers are 10th and 90th percentiles. Filled circles indicate GUD for individual days



CHAPTER 4
PERSONALITY AND SPACE USE IN FRANKLIN'S GROUND SQUIRREL
(*POLIOCITELLUS FRANKLINII*)

ABSTRACT

Personalities that are repeatable over time and multiple contexts are increasingly reported for animals living in wild populations. Studies demonstrate animal personalities may be heritable and have fitness consequences, but much work remains in relating personalities to life-history strategies in a spatial context. I used hole-board tests to characterize personalities of 55 *Poliocitellus franklinii* and then tested relationships between personality and space use of individuals. *P. franklinii* individuals demonstrated repeatable personalities characterized by vigilance and activity. For juveniles, but not adults, activity during hole-board tests was positively related to latency period before escaping a novel, risky environment. For 12 radiocollared, juvenile males, individual home range size and length of movements related negatively to vigilance and positively to activity during hole-board testing. Findings suggest vigilant and active personalities of *P. franklinii* vary in response to movement trade-offs to maximize fitness. The relationship between personality and space use for *P. franklinii* suggests personality may influence connectivity and metapopulation dynamics for this species of conservation concern in the highly fragmented grasslands of the Midwestern U.S.

Key words: Activity, behavioral syndrome, exploration, hole-board test, home range size, minimum convex polygon, temperament, vigilance

INTRODUCTION

Biologists have long sought to understand the processes underlying animal movement and habitat use, as they affect not only individual fitness, but also population dynamics, species distributions, gene flow, and adaptation (Bowler and Benton 2005; Cote et al. 2010a). Until recently, most studies considered individual variation in space-use patterns random “noise” around a population mean (Cote et al. 2010a; Dingemanse et al. 2003). However, interest in behavioral types or syndromes—animal personalities—is now renewed in the fields of ecology and evolution (Bell 2007; Dall et al. 2007; Réale et al. 2007, 2010; Sih et al. 2004a,b; Sih and Bell 2008). Tests establishing personalities that are repeatable over time and multiple contexts have been conducted on multiple taxa (Bell 2007; Dall et al. 2007; Réale et al. 2007; Sih et al. 2004a,b; Sih and Bell 2008), yet much work remains in relating personalities to life-history strategies in a spatial context (Cote et al. 2010a; Réale et al. 2010).

Most research on animal personality has focused on a few behavioral axes such as activity, exploration, and boldness, which generate trade-offs determining how animals will maximize fitness in varied contexts (i.e., foraging, mating, dispersing; Sih et al. 2004a,b). In a foraging context, for example, movement imposes travel costs and can be risky, increasing exposure to predators (Boon et al. 2008; Sih et al. 2004b). However, individuals that increase movement distances can be rewarded with access to greater and more diverse food resources (Clobert et al. 2009; Cote et al. 2010a; Wolf et al. 2007). Individuals with different personalities are likely to vary responses to movement trade-offs. An active, exploring individual might risk long-distance movements necessary to maintain a large home range, and thus maximize fitness by increasing access to food. In contrast, a less active individual might maintain a smaller home range, but maximize fitness by increasing vigilance, thereby reducing risk of predation and

increasing lifespan. Documented relationships between activity-exploration and movement generally match these expectations. For instance, latency to disperse was related negatively to activity-exploration (Krackow 2003; Torgerson 2010), whereas propensity to disperse (Holekamp 1986; Hoset et al. 2011) and home range size (Boon et al. 2008; Boyer et al. 2010) were both related positively to activity-exploration in rodents. Home range size for starlings (*Sturnus vulgaris*; Minderman et al. 2010) and dispersal distance for great tits (*Parus major*; Dingemanse et al. 2003) was also related positively to activity-exploration. Captive-bred swift foxes (*Vulpes velox*) characterized as bold traveled greater distances when reintroduced into the wild, and were less likely to survive, than foxes not considered bold (Bremner-Harrison et al. 2004). These studies, along with research on sociability and aggressiveness axes (Cote et al. 2010b; Cote and Clobert 2007, 2010; Duckworth and Badyaev 2007; Fraser et al. 2001), indicate individual variation in personality might regularly correlate with movement and habitat use, potentially influencing fitness (Boon et al. 2007, 2008; Dingemanse et al. 2003; Smith and Blumstein 2008), but replication across taxa and ecological contexts is needed in this burgeoning area of research.

I tested if personality correlated with home range size and movement distances for Franklin's ground squirrel (*Poliocitellus franklinii*). *Poliocitellus franklinii* (formerly *Spermophilus franklinii*; Helgen et al. 2009) is diurnal and lives in underground burrows in areas of tall, dense grasses. The species is secretive and considered the least social of ground squirrels (Jones and Birney 1988; Kivett et al. 1976). *P. franklinii* occurs at low densities in the Midwest and is listed as endangered in Indiana, threatened in Illinois, and a species of special concern in Iowa, Missouri, and Wisconsin. Grassland patches occupied by *P. franklinii* typically harbor ≤ 20 adult squirrels (Martin et al. 2003; Martin and Heske 2004) and are presumed

subpopulations linked by dispersal. As with other species of ground squirrels, male-biased dispersal is undertaken by juveniles in late summer and early autumn during their first year of life, preceding hibernation that extends from September - April (Reichardt and Galloway 1994). Site occupancy *P. franklinii* in the Midwestern U.S. was related positively to connectivity, and local extinction was related negatively to connectivity (Duggan et al. 2011), emphasizing the importance of movement to the long-term persistence of this species.

My study had two main objectives. First, I determined if *P. franklinii* individuals demonstrated repeatable personalities. I predicted behavior of *P. franklinii* individuals would vary along activity and exploration axes similar to other sciurids (Boon et al. 2007, 2008; Boyer et al. 2010; Martin and Réal 2008a,b). Second, I tested if personality correlated with latency to leave a risky environment, home range size, mean daily movement distance, and last movement of the season. I predicted highly active, exploratory individuals would have shorter latency to leave a risky environment, larger home ranges, and due to more or longer exploratory movements, would have longer mean daily movement than less active, exploratory individuals. Further, I predicted distance between first capture and last telemetry location would increase with activity and exploration, in accord with relationships between boldness and natal dispersal distance for non-mammalian taxa (Dingemanse et al. 2003).

MATERIALS AND METHODS

STUDY SITES AND POPULATIONS

I conducted field work from April-September 2010 on *P. franklinii* populations located in the Barnhart Prairie Nature Preserve in Champaign Co., IL and remnant prairie along a railroad right-of-way in Vermilion Co., IL. Both locations were within agricultural landscapes

and surrounded by a mosaic of corn and soybean fields, farm lots, and low-traffic roads. To capture individuals, I set Tomahawk live traps (model 202, Tomahawk Live Trap, Tomahawk, Wisconsin) baited with peanut butter and sunflower seeds, with trap number and spacing varied according to shape and extent of grassland habitat. I set traps before 0800 h, checked traps at 2-h intervals, and closed traps for the day by 1300 h. I covered traps with vegetation to protect captured squirrels from sun and light rain (traps were not opened during heavy rain). I recorded age (juvenile or adult), sex, and mass of each captured individual. From April to October 2010, I radiocollared and tracked free-living squirrels weighing >250 g using Model M 1540 transmitters with activity switches (Advanced Telemetry Systems Inc., Isanti, Minnesota) mounted on plastic cable ties. Collars each weighed 4.5 g and never exceeded 2% of body mass. I also uniquely marked individuals within each population by clipping small patches of fur, so I could identify recaptured squirrels without radiocollars. Procedures followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and the University of Illinois Institutional Animal Care and Use Committee.

HOLE-BOARD TESTS

I used a hole-board test, a modification of an open-field test, to quantify behaviors related to exploration and activity for squirrels exposed to a novel environment from which they could not escape (Boon et al. 2008; Martin and Réale 2008; Walsh and Cummins 1976). The experimental apparatus (hereafter, hole-board) was a 54 x 69 x 69 cm white wooden box with a white plastic floor containing four blind holes (5-cm diameter, 10-cm depth), each 19 cm from the center of the floor. The hole-board had a clear plexiglass lid with 19 holes (2-cm diameter) placed at 6-cm intervals around the perimeter to provide air circulation, and was always placed in

shade during tests. Because I checked traps at 2-hr intervals and had multiple captures per day, squirrels spent 0 - 4 hrs in a trap before a hole-board test. To minimize pre-test stress, I kept traps containing squirrels well-shaded and provisioned with food, and deferred collection of additional information (i.e., identification, body mass) and fitting radiocollars to squirrels until after testing. To conduct a hole-board test, I removed a squirrel from a trap using a cloth bag, immediately placed the squirrel in the center of the hole-board floor with a gloved hand, and shut the plexiglass lid to prevent escape. I recorded activity of the squirrel with a camcorder secured on a tripod above the hole-board and then returned the squirrel to its capture location. Videos were 10 min in length after ~1 min during which technicians moved > 50 m from the hole-board. Hole-board tests were typically conducted within 500 m of capture location. I cleaned the hole-board with a cloth and mixture of water and alcohol between tests.

I recorded the following behaviors from videos for each trial: head-dipping (number of times head was placed in a blind hole in floor), scanning (number of times head changed direction while rest of body remained immobile), locomotion (time in seconds walking or running), rearing (time in seconds on only hind legs), number of jumps, and number of alarm call vocalizations. For each trial, I also recorded the time and date. Hole-board tests were conducted between 1300 - 1600 h from 14 July - 27 August 2010. I quantified behaviors of 55 squirrels (9 adult females, 20 juvenile females, 5 adult males, and 21 juvenile males). Forty-five squirrels were from Champaign Co., IL and 10 were from Vermilion Co., IL. Thirty-two of 55 squirrels were tested twice, with at least 6 days between trials; the rest were not recaptured.

LATENCY-TO-ESCAPE TESTS

I devised a test to quantify the period of latency before escaping a risky environment. For this latency-to-escape test, a squirrel was placed with a gloved hand in an opaque plastic bin (32 x 48 x 42 cm) covered with a lid and set on the ground within 50 m of the location from which the squirrel was captured. A technician removed the lid and stood 1 m from the bin (visible to a squirrel standing on hind legs) while another technician standing 10 m from the bin used a stop-watch to measure the latency period between removal of the lid and escape of the squirrel from the bin. I assumed presence of a technician within 1 m of the bin, as well as exposure in an uncovered bin, presented an environment squirrels would perceive as risky. The test was run for 5 min; if a squirrel did not leave the bin within 5 min, the bin was gently tipped on its side, at which point the squirrel always left. I measured latency to escape once for 25 squirrels that had completed hole-board tests. I conducted latency-to-escape tests in Champaign Co., IL from 22 - 27 August 2010.

HOME RANGE AND MOVEMENT

From July to October 2010, I tracked 12 radiocollared, male, juvenile squirrels in Champaign Co., IL. In late August 2010, when I expected juveniles to initiate exploratory movements related to dispersal from natal ranges, I collected daily telemetry locations (between 0800 and 1700 hr). Beginning 1 September 2010, when I anticipated most dispersal movements, I collected two locations per day at consistent time intervals (0900 – 1100 hr, 1400 – 1600 hr). I obtained locations by signal homing using a receiver and handheld 3-element yagi antenna. I collected an average of 46 telemetry locations ($SE = 7$) for each squirrel. However, three squirrels had <10 locations due to death, transmitter failure, or dispersal >2 km (1 squirrel); the

remaining 9 squirrels had an average of 59 telemetry locations ($SE = 4$). I estimated home ranges with a 100% minimum convex polygons (MCP) model using Hawth's Analysis Tool for ArcGIS (Beyer 2004). Although kernel-based estimators of home range are often preferred over MCPs, kernel-based estimators do not work as well when many radiolocations occur at a small number of places (Seaman and Powell 1996), such as at burrows in this study.

I quantified movement rates of radiocollared squirrels by measuring Euclidean distances between telemetry locations for individuals using Hawth's Analysis Tool for GIS. Because duration of exploratory movements range from hours to multiple days (Martin and Heske 2005), I measured average Euclidean distance traveled between locations recorded on both the same day and from morning hours (0900 – 1100 hr) on consecutive days for each individual. To ensure movement distances were collected over comparable time periods for all individuals, I used only tracking data collected at regular time intervals in September and October 2010. Last, I measured Euclidean distance between first capture of an individual, assumed to be near a natal burrow, and last recorded location. For 7 of 12 squirrels, the last recorded location was at a burrow used as a hibernaculum. I assumed a squirrel entered hibernation if I detected <5 m movement for ≥ 3 consecutive days during October. Following this assumption, 7 radiocollared squirrels hibernated by 17 October 2010. I found collars belonging to 4 of the remaining 5 squirrels, 2 with signs suggesting predation, so I do not know if, and where, the remaining squirrels entered hibernation.

STATISTICAL ANALYSES

I used a Principal Component Analysis (PCA) to reduce correlated variables recorded during hole-board tests to a smaller number of synthetic variables. I retained principal

components with eigenvalues greater than one (Kaiser 1991). I then used the MIXED procedure (SAS 9.2, SAS Institute Inc., 2009) to test for effects of Julian date and trial (1 or 2), as well as age and sex of individual, on principal component scores, while including individual identity of a squirrel as a random effect. I used Wald Z-tests to determine significance of covariance for individual identity. These analyses allowed me to test repeatability of behaviors (proportion of total variance due to individual), while testing effects of date, trial, age, and sex on principal components (Boon et al. 2008). I then extracted best linear unbiased predictors (BLUPs) from final models, including fixed effects when significant. BLUPs predicted the random effect of each individual, independent of fixed effects in the model, and standardized to a mean of zero (Boon et al. 2008a,b, Martin and Réal 2007). I used BLUPs from each principal component as estimates of personality for each squirrel in subsequent analyses (Boon et al. 2008a,b, Martin and Réal 2007).

I used the GLIMMIX procedure (SAS 9.2, SAS Institute Inc., 2009) to test relationships between behavior profiles (BLUPs) and latency to escape a risky environment, home range size, mean movement distances within days and between consecutive days, and distance between first and last location. For analysis of latency to escape, I included age and sex as fixed effects but not date, as all tests were conducted within a 5-day period. Because MCP home range estimates can be dependent on sample size (Borger et al. 2006; Boyle et al. 2009; Laver and Kelly 2008), I included number of radiotelemetry locations as a fixed effect when testing the relationship between behavior profiles and home range size. For all analyses, I used a gamma distribution and a log link, and estimated degrees of freedom using the Kenward-Roger method. Due to moderate sample sizes, I considered effects significant at $P < 0.10$ for all analyses.

RESULTS

HOLE-BOARD TESTS

I retained three principal components from PCA that together explained 67% of total variance (Table 3.1). The first component was correlated positively with head-dipping and locomotion (hereafter termed exploration), the second with head scanning and alarm call vocalizations (vigilance), and the third with rearing and jumping (activity; Table 3.1). Wald-Z tests indicated proportions of total variance due to individual for vigilance (Covariance = 0.72, $SE = 0.19$, $Z < 0.001$) and activity (Covariance = 0.60, $SE = 0.16$, $Z < 0.001$) were significant, demonstrating repeatability of these personality traits, but repeatability of exploration was low (Covariance = 0.08, $SE = 0.20$, $Z > 0.35$; Table 3.1). Trial number was the only significant fixed effect on behaviors; squirrels decreased exploration (Covariance = 0.92, $SE = 0.23$, $P < 0.001$), vigilance (Covariance = 0.33, $SE = 0.08$, $P < 0.001$), and activity (Covariance = 0.36, $SE = 0.08$, $P < 0.001$) with repeated testing. Therefore, I retained trial as a fixed factor in final models used to extract BLUPs. Because exploration was not repeatable for individuals, I included only BLUPs extracted for vigilance and activity in models. Inclusion of BLUPS extracted for exploration produced qualitatively similar results but are not reported.

LATENCY-TO-ESCAPE TESTS

Juvenile squirrels (mean = 57.3, $SE = 24.8$ s) escaped more quickly than adults (mean = 113.3, $SE = 47.5$ s; $F_{1,19} = 14.04$, $P < 0.001$). Latency to escape increased with activity ($F_{1,19} = 10.14$, $P < 0.005$); however, an interaction between age and activity included in a post hoc model indicated latency period increased with greater activity for juveniles, but not for adults ($F_{1,19} = 10.57$, $P < 0.004$; Fig. 1).

HOME RANGE AND MOVEMENT

Home range size for juvenile males (mean = 2.04 ha, $SE = 0.77$) increased with number of telemetry locations for an individual ($F_{1,8} = 27.85$, $P < 0.001$), decreased with vigilance ($F_{1,8} = 3.41$, $P < 0.10$), and increased with activity ($F_{1,8} = 3.86$, $P < 0.09$; Fig. 2). Whereas distance between locations for squirrels within a day (mean = 60 m, $SE = 11$) decreased with vigilance ($F_{1,7} = 4.09$, $P < 0.08$; Fig. 3), distance between locations during consecutive days (mean = 47 m, $SE = 10$) did not vary with vigilance ($F_{1,8} = 2.09$, $P > 0.19$). Distance between first and last location (mean = 319 m, $SE = 168$) decreased with vigilance ($F_{1,9} = 5.20$, $P < 0.05$) and increased with activity for all radiotracked individuals ($F_{1,9} = 8.43$, $P < 0.07$; Fig. 4). For a subset of individuals for which I confirmed last location as hibernacula, mean distance between first and last location did not vary with vigilance, but increased with activity ($N = 7$, $F_{1,4} = 5.41$, $P < 0.08$; Fig. 4).

DISCUSSION

P. franklinii is a secretive species found at low densities throughout the highly fragmented grasslands of the Midwestern U.S. Populations are presumed connected primarily by male-biased natal dispersal, but few studies have examined predictors of area use or movement in this species (Martin and Heske 2005). During hole-board tests, *P. franklinii* individuals demonstrated personalities characterized by vigilance and activity that were repeatable over time. Additionally, personalities for *P. franklinii* individuals were associated with space use and movement in the wild. For juveniles, but not adults, activity during hole-board tests was positively related to latency period before escaping a novel, risky environment. Juvenile males

that were vigilant during hole-board testing had the smallest home ranges and shortest movements, whereas active juvenile males had the largest home ranges and longest movement distances between first capture and last location recorded using telemetry. Findings suggest vigilant and active personalities of *P. franklinii* vary in response to movement trade-offs, and given an isometric relationship between home range size and dispersal distance for mammals (Bowman et al. 2002), may potentially be used to predict area use and dispersal distance for this species.

Based on previous studies quantifying behavior for sciurids I expected most variance in *P. franklinii* activity during hole-board tests would be explained by exploration (Boon et al. 2008a,b; Boyer et al. 2010; Martin and Réale 2008). In fact, this was the case. However, exploration was not repeatable for *P. franklinii*. Although squirrels reduced all behaviors with repeated trials (i.e., habituated to the hole-board; Martin and Réale 2008), exploration decreased to the extent that it was not useful in characterizing personality of individuals. Although *P. franklinii* might demonstrate repeatable exploration in a different behavioral test, possibly the steep decrease in this behavior was indicative of the natural history of the species. The vigilance and activity expressed by *P. franklinii* during hole-board tests resembles reactive and proactive coping styles demonstrated by laboratory rodents tested for responses to stress (Koolhaas 2008; Koolhaas et al. 1997, 1999). Perhaps secretive, asocial species are better characterized by stress responses than exploratory, bold, or aggressive behaviors. Indeed, during preliminary mirror-image stimulation tests (Armitage and van Vuren 2003; Boon et al. 2008a,b), *P. franklinii* individuals did not respond to mirrors, suggesting individuals might not be well characterized by an aggression axis (J. M. Duggan, Pers. Obs.). Quantifying behavior across a wider range of

species should reveal more general relationships between personality and natural history of a species.

For juveniles, latency was related positively with activity, which was also positively associated with home range size and distance between first and last location. It seems paradoxical that the individuals most likely to move the longest distances also had the longest periods of latency before leaving a novel environment. My measure of activity in hole-board tests, rearing and jumping, suggested high anxiety and eagerness to escape a perceived risky environment. However, my latency-to-escape test may have presented squirrels with an environment that, due to the presence of a visible, potential predator (a human), was at first perceived as even more risky than the novel bin environment in which they started the test, causing hesitancy in leaving. Thus, although one interpretation of greater rearing and jumping during the hole-board tests might be boldness, another might be even greater levels of anxiety than expressed by individuals that demonstrated more vigilance. Alternatively, juveniles of some species, including rodents such as *Spermophilus beldingi* (Belding's ground squirrel; Holekamp 1986) and *Microtus oeconomus* (root voles; Hoset et al. 2011) sometimes temporarily change behavior before dispersal. For example, *S. beldingi* decreased exploratory behaviors during the week in which dispersal occurred, possibly because stress associated with preparation for dispersal interfered with exploratory behaviors (Holekamp 1986); perhaps juvenile *P. franklinii* do the same. Although both juveniles and adults were characterized by vigilance and activity during hole-board tests, only juveniles demonstrated a relationship between activity and latency in escaping the experimental bin. I also found no relationship between activity and latency in homing for adult squirrels released in a gap-crossing experiment conducted at the same site earlier in the year.

I predicted positive relationships between activity and exploration for juvenile, male *P. franklinii* and home range size and movement distances. As expected, active individuals had the largest home ranges and longest final movements of the season, but home range size and length of last movements of the season were also negatively related to vigilance. I also predicted activity and exploration during hole-board testing would relate positively with more or longer movements (i.e., activity) in the wild, resulting in a positive association with mean daily movement distance. However, mean daily movement distance was not associated with activity or exploration, but rather was related negatively to vigilance. Together, these results suggest individuals with active personalities responded to movement trade-offs by increasing home range size, and potential access to food and nesting resources, whereas vigilant squirrels decreased home range size and movement, potentially decreasing exposure to predators. Interestingly, the lack of relationship between activity and mean daily movement distance suggests individuals demonstrating activity during hole-board testing may not have increased frequency or length of movements as expected before dispersing. Selonen and Hanski (2006) found *Pteromys volans* (Siberian flying squirrel) individuals that dispersed the farthest explored the least before travel. Long-distance dispersers in *P. volans* typically dispersed beyond a distance they could explore before beginning travel, and thus individuals with a propensity for dispersal did not explore because doing so would be of little benefit (Selonen and Hanski 2006). *P. franklinii* may follow a similar pattern. Only one of my radiocollared individuals dispersed >700 m, and this individual dispersed relatively early (between 20 August and 1 September 2010) with no recorded exploratory movements.

In this study, *P. franklinii* individuals expressed repeated behaviors in controlled behavioral tests that were related to behaviors in the wild. Personality was related to home range

size, demonstrating understanding of the spatial ecology of this rare species could be enhanced by studying the heritability of personality and its effect on fitness (Boon et al. 2008a,b; Dingemanse et al. 2003; Smith and Blumstein 2008). Personality was also related to movement distances, suggesting a potential role in connectivity and metapopulation dynamics for *P. franklinii* in the highly fragmented grasslands of the Midwestern U.S. The personality of dispersers may influence genetic composition of populations across a landscape, and could have consequences for which populations will persist through time, especially with changes in environment (i.e., food resources, predation risk) that alter movement tradeoffs (Cote et al. 2010a). For a species of conservation concern, such as *P. franklinii*, a better understanding of behavior, and its relationship to spatial ecology, may promote improved management and conservation strategies.

ACKNOWLEDGMENTS

I am grateful to the Barnhart family for allowing me to radiotrack squirrels on private property adjacent to the Barnhart Prairie Nature Preserve. I thank S. Fredebaugh-Siller, L. Pritchard, and J. Rydzewski for field assistance. This project was funded by the Illinois Department of Natural Resources through the Federal Aid in Wildlife Restoration Program (Project W-152-R) and the University of Illinois.

REFERENCES

- ARMITAGE, K. B., AND D. H. VAN VUREN. 2003. Individual differences and reproductive success in yellow-bellied marmots. *Ethology, Ecology, and Evolution* 15:207-233.
- BELL, A. 2007. News and views: animal personalities. *Nature* 447: 539-540.
- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatialecology.com/htools>.
- BOON, A. K., D. RÉALE, AND S. BOUTIN. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters* 10:1094-1104.
- BOON, A. K., D. RÉALE, AND S. BOUTIN. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321-1328.
- BORGER, L., N. FRANCONI, F. FERRETTI, F. MESCHI, G. DE MICHELE, A. GANTZ, AND T. COULSON. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist* 168:471-485.
- BOWLER, D. E., AND T. G. BENTON. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biology Review* 80:205-225.
- BOWMAN, J., J. A. G. JAEGER, AND L. FAHRIG. 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83:2049-2055.
- BOYER, N., D. RÉALE, J. MARMET, B. PISANU, AND J.-L. CHAPUIS. 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology* 79:538-547.

- BOYLE, S. A., W. C. LOURENCO, L. R. DA SILVA, AND A. T. SMITH. 2009. Home range estimates vary with sample size and methods. *Folia Primatol* 80:33-42.
- BREMNER-HARRISON, S., P. A. PRODOHL AND R. W. ELWOOD. 2004. Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation* 7:313-3320.
- CLOBERT, J., J.-F. LE GALLIARD, J. COTE, S. MEYLAN, AND M. MASSOT. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197-209.
- COTE, J., AND J. CLOBERT. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society, B. Biological Sciences* 274:383–390.
- COTE, J., AND J. CLOBERT. 2010. Risky dispersal: avoiding kin competition despite uncertainty. *Ecology* 91:1485-1493.
- COTE, J., J. CLOBERT, T. BRODIN, S. FOGARTY, AND A. SIH. 2010a. Personality-dependent dispersal: ontogeny and consequences for spatially-structured populations. *Philosophical Transactions of the Royal Society, B. Biological Sciences* 365:4065-4076.
- COTE, J., S. FOGARTY, K. WEINERSMITH, T. BRODIN, T., AND A. SIH. 2010b. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society, B. Biological Sciences* 277:1571–1579.
- DALL, S. R. X., A. I. HOUSTON, AND J. M. MCNAMARA. 2007. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* 7:734-739.

- DINGEMANSE, N. J., C. BOTH, A. J. VAN NOORDWIJK, A. L. RUTTEN, AND P. J. DRENT. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society, B. Biological Sciences 270:741–747.
- DUCKWORTH, R. A., AND A. V. BADYAEV. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences of the United States of America. 104:15017-15022.
- DUGGAN, J. M., R. L. SCHOOLEY, AND E. J. HESKE. 2011. Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecology In press.
- FRASER, D. F., J. F. GILLIAM, M. J. DALEY, A. N. LE, AND G. T. SKALSKI. 2001. Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. The American Naturalist 158:124-135.
- HELGEN, K. M., F. R. COLE, L. E. HELGEN, AND D. E. WILSON. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. Journal of Mammalogy 90:270-305.
- HOLEKAMP, K. E. 1986. Proximal Causes of Natal Dispersal in Belding's Ground Squirrels (*Spermophilus Beldingi*). Ecological Monographs 56:365-391.
- HOSSET, K. S., A.-L. FERCHAUD, F. DUFOUR, D. MERSCH, J. COTE, AND J.-F. LE GALLIARD. 2011. Natal dispersal correlates with behavioral traits that are not consistent across early life stages. Behavioral Ecology 22:176-183.
- JONES, J. K., JR., AND E. C. BIRNEY. 1988. *Spermophilus franklinii*. Pp. 160–161 in Handbook of mammals of the north central states (M. R. Davis, ed.). University of Minnesota Press, Minneapolis, Minnesota.

- KAISER, H. F. 1991. Coefficient alpha for a principal component and the Kaiser-Guttman rule. *Psychological Reports* 68:855-858.
- KIVETT, V. K., J. O. MURIE, AND A. L. STEINER. 1976. A comparative study of scent-gland location and related behavior in some northwestern Nearctic ground squirrel species (Sciuridae): an evolutionary approach. *Canadian Journal of Zoology* 54:1294–1306.
- KOOLHAAS, J. M. 2008. Coping style and immunity in animals: making sense of individual variation. *Brain, Behavior, and Immunity* 22:662-667.
- KOOLHAAS, J. M., S. F. DE BOER, B. BOHUS. 1997. Motivational systems and motivational states: behavioural and physiological evidence. *Applied Animal Behaviour Science* 53:131-143.
- KOOLHAAS, J. M., S. M. KORTE, S. F. DE BOER, B. J. VAN DER VEGT, C. G. VAN REENEN, H. HOPSTER, I. C. DE JONG, M. A. W. RUIS, AND H. J. BLOKHUIS. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews* 23:925-935.
- KRACKOW, S. 2003. Motivational and inheritable determinants of dispersal latency in wild male house mice (*Mus musculus musculus*). *Ethology* 109:671-689.
- LAVER, P. N., AND M. J. KELLY. 2008. A critical review of home range studies. *Journal of Wildlife Management* 72:290-298.
- MARTIN, J. M., AND E. J. HESKE. 2004. Cover and soil drainage influence burrow location of Franklin's ground squirrel (*Spermophilus franklinii*) in Champaign County, Illinois. *Transactions of the Illinois State Academy of Science* 97:227-233.

- MARTIN, J. M., AND E. J. HESKE. 2005. Juvenile dispersal of Franklin's ground squirrel (*Spermophilus franklinii*) from a prairie "island". *American Midland Naturalist* 153:444–449.
- MARTIN, J. M., E. J. HESKE, AND J. E. HOFMANN. 2003. Franklin's ground squirrel in Illinois: a declining prairie mammal? *American Midland Naturalist* 150:130–138.
- MARTIN, J. G. A., AND D. RÉALE. 2008a. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 75:309–318.
- MARTIN, J. G. A., AND D. RÉALE. 2008b. Animal temperament and human disturbance: implications for the response on wildlife to tourism. *Behavioural Processes* 77:66–72.
- MINDERMAN, J., J. M. REID, M. HUGHES, M. J. H. DENNY, S. HOGG, P. G. H. EVANS, AND M. J. WHITTINGHAM. 2010. Novel environment exploration and home range size in starlings *Sturnus vulgaris*. *Behavioral Ecology* 21:1321–1329.
- RÉALE, D., S. M. READER, D. SOL, P. T. MCDUGALL, AND N. J. DINGEMANSE. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- RÉALE, D., N. J. Dingemanse, A. J. N. Kazem, and J. Wright. 2010. Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society, B. Biological Sciences* 365:3937–3946.
- REICHARDT, T. R., AND T. D. GALLOWAY. 1994. Seasonal occurrence and reproductive status of *Opisocrostitis bruneri* (Siphonaptera: Ceratophyllidae), a flea on Franklin's ground squirrel, *Spermophilus franklinii* (Rodentia: Sciuridae) near Birds Hill Park, Manitoba. *Journal of Medical Entomology* 31:105–113.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.

- SELONEN, V., AND I. K. HANSKI. 2006. Habitat exploration and use in dispersing juvenile flying squirrels. *Journal of Animal Ecology* 75:1440-1449.
- SIH, A., AND A. M. BELL. 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behaviour* 38:227–281.
- SIH, A., A. BELL, AND J. C. JOHNSON. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution*. 19:372–377.
- SIH, A., A. BELL, J. C. JOHNSON, AND R. E. ZIEMBA. 2004b. Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology* 79:241-277.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.
- SMITH, B. R., AND D. T. BLUMSTEIN. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19:448-455.
- TORGERSON, L. L. 2010. Personality in Michigan's *Peromyscus*. M.S. Thesis., Michigan State University, East Lansing, Michigan.
- WALSH, R. N., AND R. A. CUMMINS. 1976. The open-field test: a critical review. *Psychology Bulletin* 83:482–504.
- WOLF, M., G. SANDER VAN DOORN, O. LEIMAR, AND F. J. WEISSING. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584.

TABLES AND FIGURES

Table 4.1 PCA loadings for behaviors collected from hole-board tests of 55 Franklin's ground squirrels (32 squirrels were tested twice) from populations in Champaign and Vermilion Counties, IL. Locomotion and rearing behaviors were measured in seconds. All other behaviors were recorded as count data.

Behavioral variables	Component 1: Exploration	Component 2: Vigilance	Component 3: Activity
Head-dipping	0.820	-0.104	0.026
Locomotion	0.783	0.255	-0.162
Alarm calls	-0.139	0.865	-0.105
Scanning	0.350	0.710	0.180
Jumping	0.129	-0.060	0.806
Rearing	-0.265	0.090	0.674
% total variance	25.2	22.4	19.6
% repeatability	7.7	72.2	59.8

FIGURE 4.1 Relationship between activity, as predicted by best linear unbiased predictors (BLUPs), and latency to escape from a novel, risky environment for A) adult and B) juvenile Franklin's ground squirrels. Hole-board tests were conducted July-August 2010 in Champaign and Vermilion Co., IL. Latency-to-escape tests were conducted from 22 - 27 August in Champaign Co., IL.

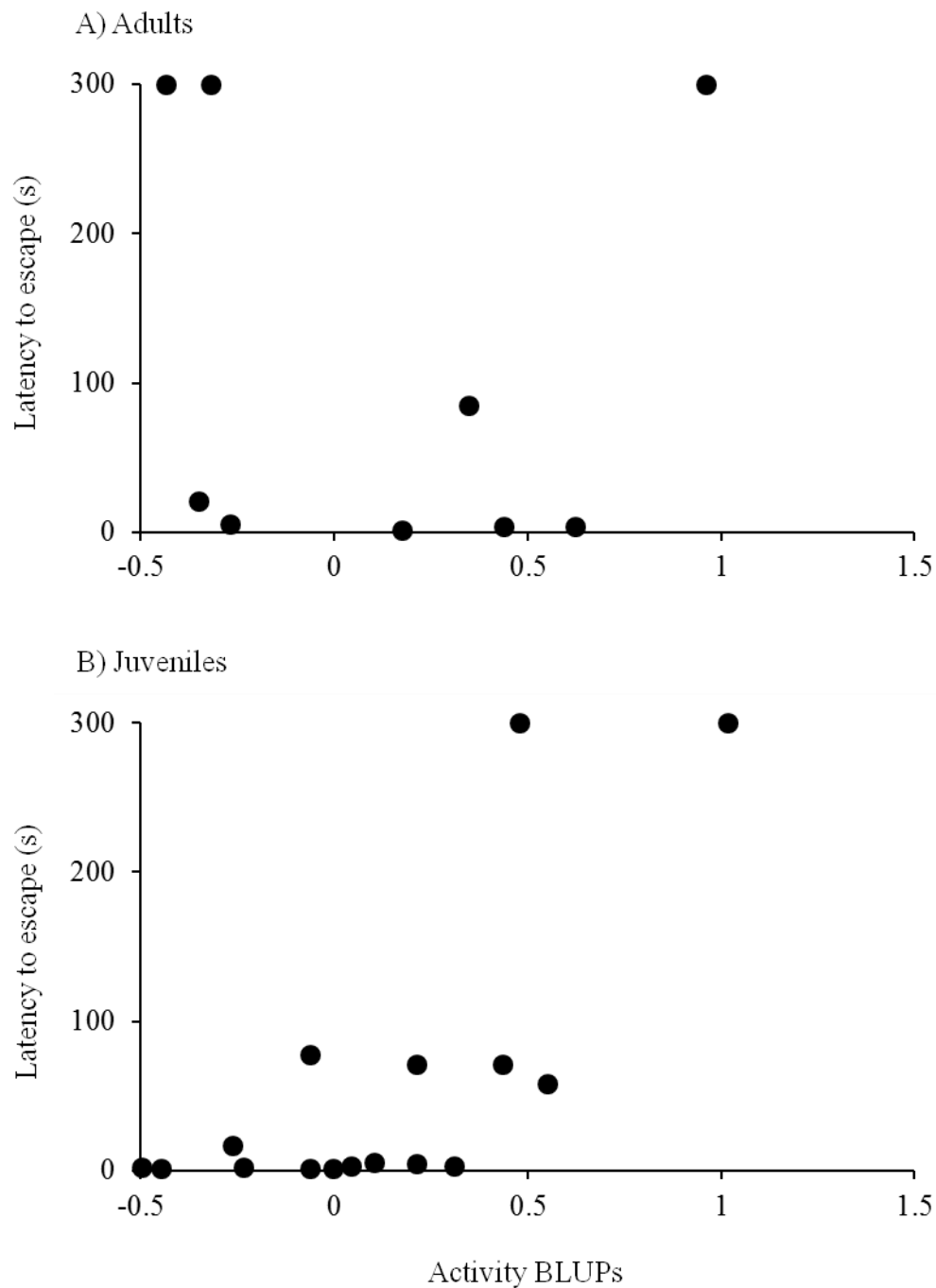


FIGURE 4.2 Relationship between A) vigilance and B) activity, as predicted by best linear unbiased predictors (BLUPs), and home range size (ha). Home range size was estimated using 100% minimum convex polygons (MCP) models for male, juvenile Franklin's ground squirrels radiotracked July – October 2010 in Champaign Co., IL. Hole-board tests were conducted July - August 2010 in Champaign and Vermilion Co., IL.

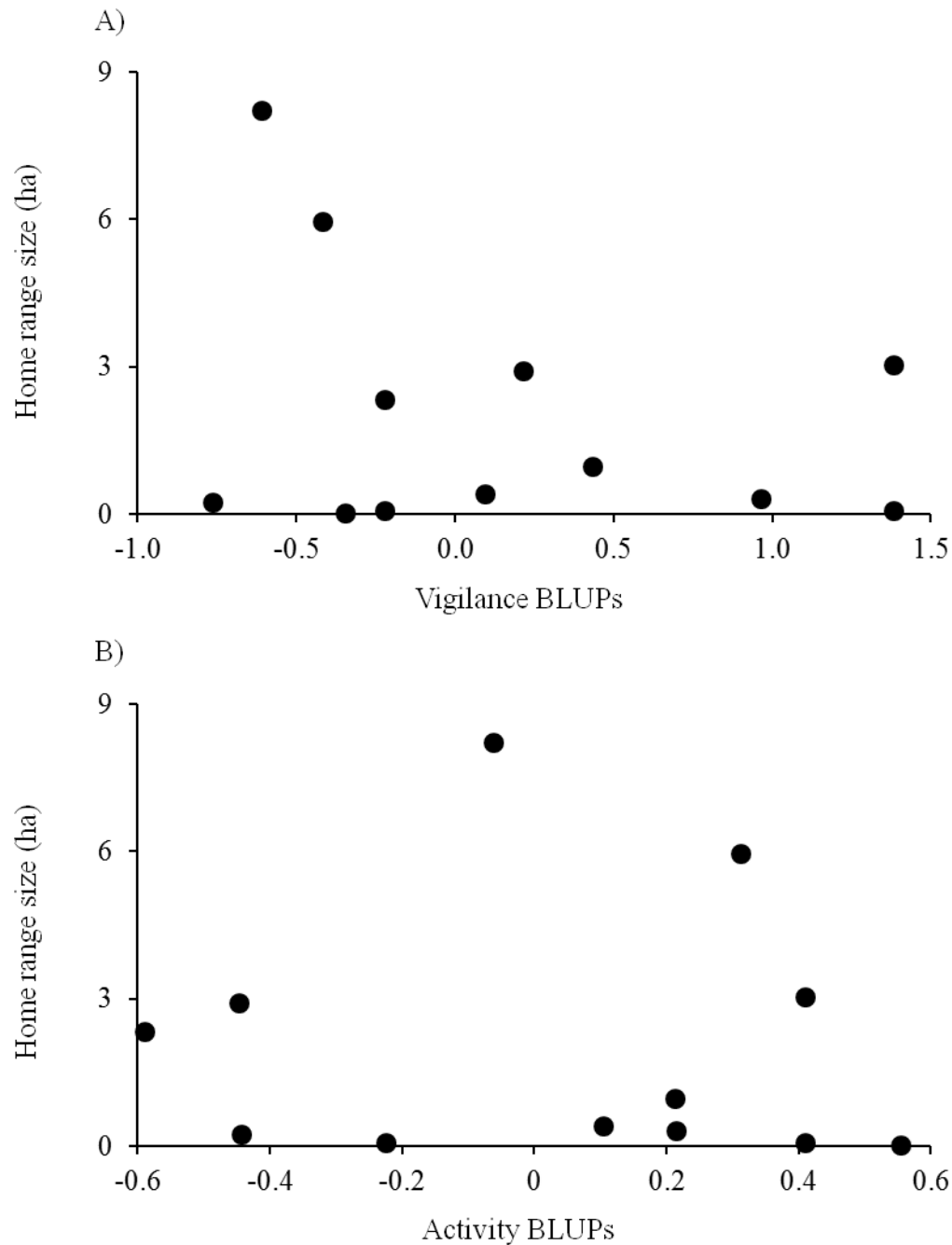


FIGURE 4.3 Relationship between vigilance, as predicted by best linear unbiased predictors (BLUPs), and average Euclidean distance between consecutive telemetry locations recorded within a day for male, juvenile Franklin's ground squirrels. Hole-board tests were conducted July - August 2010 in Champaign and Vermilion Co., IL.

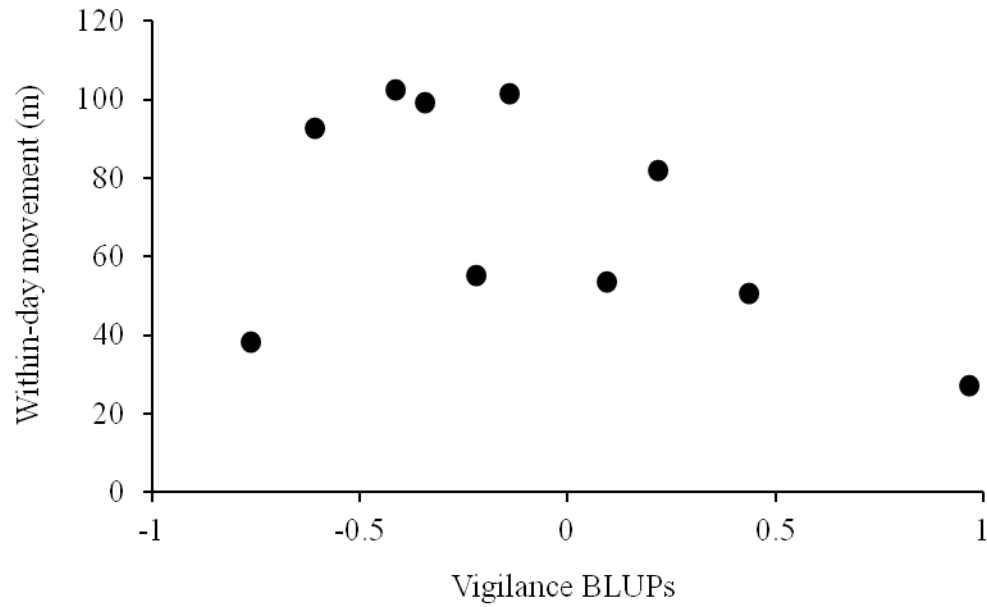
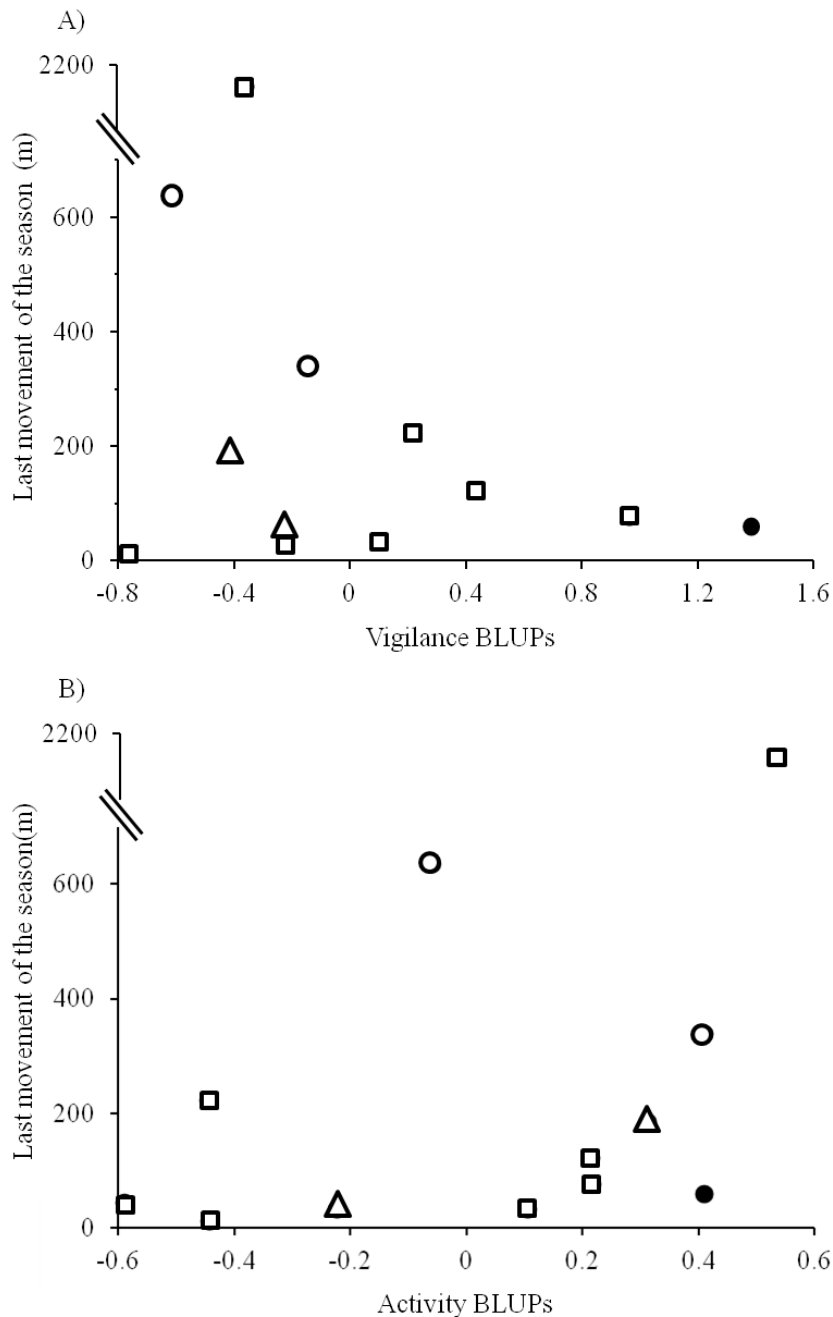


FIGURE 4.4 Relationship between A) vigilance and B) activity, as predicted by best linear unbiased predictors (BLUPs), and Euclidean distance between first and last location recorded. Male, juvenile Franklin's ground squirrels were radiotracked July – October 2010 in Champaign Co., IL. Hole-board tests were conducted July - August 2010 in Champaign and Vermilion Co., IL. Open squares = last location for individuals that entered hibernacula, open triangles = last location for individuals assumed depredated, open circle = last location for radiocollars found without sign of depredation, filled circles = last location for individual with unknown fate



APPENDIX A

General location, site number, type of study site (Road = roadside, Reserve = prairie reserve, RR = railroad right-of-way), date of last record of *Polioctellus franklinii* capture or sighting, and number of *P. franklinii* captured for 55 study sites from 2007-2009.

Location	Site	Type	Last Record	2007	2008	2009
Champaign Co., IL	1	Road	.	0	0	0
Champaign Co., IL	2	Road	2006	1	1	0
Champaign Co., IL	3	Reserve	.	0	1	0
Champaign Co., IL	4	Road	.	3	2	4
Champaign Co., IL	5	Road	.	0	1	0
Champaign Co., IL	6	Road	.	0	0	0
Champaign Co., IL	7	Road	.	0	0	0
Champaign Co., IL	8	Reserve	2006	11	8	5
Sangamon Co., IL	1	Road	2006	5	2	0
Sangamon Co., IL	2	RR	2006	9	1	2
Sangamon Co., IL	3	Road	.	1	1	2
Sangamon Co., IL	4	Road	.	0	0	0
Sangamon Co., IL	5	RR	.	0	0	0
Vermilion Co., IL.	1	Road	.	0	0	0
Vermilion Co., IL.	2	Road	.	0	0	0
Vermilion Co., IL.	3	RR	2001	6	3	2
Vermilion Co., IL.	4	RR	.	0	2	2
Vermilion Co., IL.	5	RR	2001	4	4	1
Vermilion Co., IL.	6	RR	.	7	8	6
Vermilion Co., IL.	7	RR	.	0	0	0
Wayne Co., IA	1	Road	.	0	0	0
Wayne Co., IA	2	Road	.	2	0	0
Wayne Co., IA	3	RR	.	0	0	0
Wayne Co., IA	4	Road	.	1	0	0
Wayne Co., IA	5	Road	2006	5	9	5
Wayne Co., IA	6	Road	.	0	0	0
Wayne Co., IA	7	Road	.	0	0	0

Appendix A (continued)

Benton Co., IN	1	RR	1986	1	0	0
Benton Co., IN	2	RR	1987	2	0	1
Benton Co., IN	3	RR	.	0	0	1
Benton Co., IN	4	RR	1986	0	0	0
Benton Co., IN	5	RR	1987	0	0	0
Benton Co., IN	6	RR	.	0	0	0
Benton Co., IN	7	RR	1987	0	0	0
Daviess Co., MO	1	Road	.	0	0	0
Daviess Co., MO	2	Road	.	1	0	0
Daviess Co., MO	3	Road	2001	1	0	0
Daviess Co., MO	4	Road	.	0	0	0
Daviess Co., MO	5	Road	2001	0	0	0
Daviess Co., MO	6	Road	.	0	0	0
Daviess Co., MO	7	Road	.	0	0	0
Holt Co., MO	1	Road		0	0	1
Holt Co., MO	2	RR	.	1	2	0
Holt Co., MO	3	Road	2001	2	4	0
Holt Co., MO	4	Road	2001	0	2	0
Holt Co., MO	5	Road	.	1	0	0
Holt Co., MO	6	Road	.	0	0	0
Holt Co., MO	7	Road	.	0	0	2
Nodaway Co., MO	1	Reserve	2004	0	0	0
Nodaway Co., MO	2	Road	.	0	0	0
Nodaway Co., MO	3	Reserve	2004	1	0	0
Nodaway Co., MO	4	Reserve	2004	0	2	1
Nodaway Co., MO	5	Reserve	2004	2	0	1
Nodaway Co., MO	6	Road	.	0	0	0
Nodaway Co., MO	7	Road	.	0	0	0

APPENDIX B

Field-crossing decisions and homing (returning to a home range within 24 hrs of translocation release) for 17 adult *Poliocitellus franklinii* in 33 translocations across crop fields. Potential predictors included date, individual (ID), sex, trial, body mass, location, crop height, crossing distance (Euclidean distance between center of home range and release location), detour distance (shortest distance from release point to center of home range avoiding crop field), and detour efficiency (crossing distance divided by detour distance).

Date	ID	Sex	Trial	Mass (g)	Location	Crop height (cm)	Crossing distance (m)	Detour distance (m)	Detour efficiency	Decision	Homing
05/01/10	1	Male	1	430	Champaign	0	208	236	0.88	Detour	Yes
05/04/10	1	Male	2	437	Champaign	0	705	859	0.82	Cross	Yes
06/19/10	2	Female	1	490	Champaign	30	220	277	0.79	Cross	Yes
06/09/10	3	Male	1	531	Champaign	10	268	268	1.00	Detour	Yes
06/25/10	3	Male	2	524	Champaign	30	549	637	0.86	Detour	No
05/30/10	4	Male	1	480	Vermilion	20	987	1290	0.77	Detour	Yes
06/07/10	4	Male	2	465	Vermilion	10	1527	1607	0.95	Detour	Yes
06/11/10	5	Male	1	505	Champaign	20	291	370	0.79	Detour	Yes
06/24/10	5	Male	2	493	Champaign	30	289	373	0.78	Detour	Yes
06/30/10	5	Male	3	496	Champaign	40	393	551	0.71	Detour	Yes
05/06/10	6	Female	1	294	Champaign	0	472	622	0.76	Cross	Yes
05/09/10	6	Female	2	306	Champaign	0	201	302	0.66	Detour	Yes
05/24/10	7	Male	1	522	Vermilion	10	306	315	0.97	Detour	Yes
06/17/10	8	Female	1	431	Champaign	20	631	780	0.81	Detour	Yes
06/16/10	9	Male	1	462	Champaign	20	722	952	0.76	Detour	Yes
06/18/10	9	Male	2	456	Champaign	30	387	691	0.56	Detour	Yes
07/05/10	9	Male	3	506	Champaign	40	387	691	0.56	Cross	Yes
05/18/10	10	Male	1	450	Vermilion	0	277	313	0.89	Detour	Yes
05/29/10	10	Male	2	462	Vermilion	20	883	919	0.96	Detour	No
05/22/10	11	Female	1	411	Vermilion	10	220	608	0.36	Detour	Yes
05/26/10	11	Female	2	422	Vermilion	20	447	1023	0.44	Detour	Yes
04/30/10	12	Female	1	286	Champaign	0	87	87	1.00	Cross	Yes
05/09/10	12	Female	2	294	Champaign	0	870	1057	0.82	Cross	No
06/10/10	13	Female	1	430	Champaign	10	426	538	0.79	Detour	No
06/12/10	13	Female	2	429	Champaign	20	193	197	0.98	Detour	Yes
06/13/10	13	Female	3	428	Champaign	20	250	299	0.84	Detour	Yes
05/01/10	14	Female	1	405	Champaign	0	184	209	0.88	Detour	Yes
05/14/10	14	Female	2	457	Champaign	0	582	957	0.61	Detour	Yes
05/19/10	15	Female	1	442	Vermilion	0	357	732	0.49	Cross	Yes
05/27/20	15	Female	2	502	Vermilion	20	592	1042	0.57	Detour	Yes
05/19/10	16	Male	1	447	Vermilion	0	616	630	0.98	Detour	Yes
06/06/10	16	Male	2	469	Vermilion	20	315	338	0.93	Cross	Yes
06/21/10	17	Female	1	415	Champaign	30	653	911	0.72	Detour	No